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Saproxylic beetle (Coleoptera) communities and forest management practices in coniferous stands in southwestern Nova Scotia, Canada

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Abstract

Old-growth forests in Nova Scotia typically exhibit an uneven-aged, multi-layered stand structure and contain significant amounts of coarse woody debris. Many forest species, including invertebrates, depend in various ways on deadwood substrates. The objective of this study was to investigate relationships between forest stand age, silvicultural treatment, dead wood, and invertebrate biodiversity, using saproxylic beetles as an indicator group. Saproxylic beetle communities were also compared in the context of other studies in Nova Scotia. Beetles were gathered using four collection techniques: pitfall traps, funnel traps, sweep-netting, and manual searching. Results show that both stand age and harvest treatment had an effect on species richness and species composition. Younger stands had lower species richness and hosted a significantly different suite of species than medium-aged or older ones. Similarly, harvested stands had lower species richness and were host to a significantly different suite of species than unharvested stands. The results from the investigation of stand age are of particular interest. Forest management that disregards the dependence of different suites of beetles on forest stands of various ages and compositions, emphasizing even-aged single-species stands, may be harmful to the species diversity of Nova Scotia's forest ecosystems.

Keywords

Coleoptera, saproxylic, forest management, coarse woody debris, dead wood, coniferous forests, biodiversity, forest stand age, silvicultural treatment, Nova Scotia, Canada

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Introduction

Many indicators have been developed for monitoring forest health and human impacts on forest ecosystems (Noss 1999). Communities of invertebrates are especially useful for monitoring environmental change. Several attributes make them particularly useful indicators including, ease of collection, functional importance, high site specificity, and known taxonomy (Langor and Spence 2006; Oliver and Beattie 1996a). A frequently suggested indicator is the diversity of saproxylic beetles.

Saproxylic beetles are a functional group of Coleoptera that depend, at some point in their life cycle, on dead or decaying wood or fungi associated with deadwood (Speight 1989; Økland et al. 1996). Not only do these insects comprise a large proportion of total forest species richness, but they also play an important role in decomposition and nutrient cycling in forest ecosystems (Siitonen 2001; Grove 2002b). Saproxylic beetles are considered pioneers as they are often the first to colonize dead wood. Early colonization by wood-boring species is thought to precondition the wood for succeeding species (Hammond et al. 2001). Saproxylic beetles are, in large part, responsible for the mechanical breakdown of coarse woody debris (CWD) (Hickin 1963). These beetles also demonstrate sensitivity to timber-harvest practices (Simila et al. 2002).

Nova Scotia forests have been subjected to a long history of human activity (Lynds 1989). This ranges from land clearing by early settlers, to forest "highgrading" between the 17th and 19th centuries, and finally clearcutting by the timber industry (Lynds 1989). Due to intensive management, 91% of the forested landscape is made up of young (less than 100 years) even-aged stands (Stewart et al. 2003). Few examples of really old forests with canopy trees of 250-300+ years old still exist. Although 73% of the land base is forested, no more than 0.6% of that land is comprised of old-growth forests (McMahon 1989; Loo and Ives 2003).

Nova Scotian old-growth forests (defined herein as being dominated by canopy trees over 120 years old) are typically comprised of uneven-aged, multi-layered stand structures and contain large quantities of CWD (Stewart et al. 2003). Thompson (2004) conducted an analysis of the CWD in southwestern Nova Scotia and found that mean stand volumes of CWD were relatively higher in old stands as compared to young and mid-aged stands. CWD volumes were higher in partially-harvested stands than in the unharvested stands of the same age class, but only in young stands.

Although old growth stands are rare in the Acadian forest region, their contribution to biodiversity may be significant (Loo and Ives 2003; Stewart et al. 2003; McMullin et al. 2008). The structural heterogeneity provided by CWD in forest ecosystems also gives rise to a wide range of ecological niches at the small-scale level. CWD and other deadwood materials in forests provide a multitude of habitats for numerous plant and animal species (Speight 1989; Franklin 1990; Grove 2002a). Although the study of saproxylic insects in the Maritime Provinces is relatively young, and old-growth forests have been little investigated in this regard, there are already preliminary indications that these same principals apply to forests in this region. Majka and Pollock (2006) reported the results of four studies of forest beetles that found between 54 and 76% of

forest species were saproxylic. Majka (2007b) examined 14 families, subfamilies, and tribes of saproxylic beetles and found 59 apparently rare species that comprise 33% of the 178 species within these groups – a large proportion of the saproxylic fauna. Majka (2007b) proposed that this apparent scarcity might be due to the history of forest management practices in the region. These preliminary indications of the importance of saproxylic beetles, the scarcity of many species, and the very low fraction of old-growth forests in the region, together suggest that the virtual disappearance of microhabitats found in old growth forests may have affected a substantial proportion of Nova Scotia's native saproxylic species.

There are few studies of saproxylic invertebrates in eastern Canada compared to many areas of northern Europe (Jonsell et al. 1998; Kaila et al. 1997; Kolmstrom and Lumatjarvi 2000; Kouki et al. 2000; Martikainen 2001; Martikainen and Kouki 2003; Martikainen et al. 2000; Muona 1999; Økland et al. 1996; Rainius and Jansson 2002; Siitonen 1994, 2001; Simila et al. 2002, 2003; Sverdrup-Thygeson and Ims 2002; Vaisanen et al. 1993). Only in the last decade have serious investigations of the Nova Scotia saproxylic fauna been undertaken. Bishop (1998) and Bishop et al. (in press) highlighted the relationship between forest disturbance and saproxylic beetles. The relationship between forest disturbance, whether anthropogenic or not, and saproxylic beetle diversity is of growing importance. The principal goal of this study was to determine how saproxylic beetle communities vary with forest stand age and silvicultural treatment in mature conifer stands in southwestern Nova Scotia. These relationships were studied indirectly through the relationship between dead wood and beetle diversity. Other objectives were to define habitat for saproxylic species, mainly by qualitative and quantitative examination of CWD, and to contribute to a baseline understanding of the composition of forest-beetle communities in the Maritime Provinces.

Methods

Study area

The present study focused on shade tolerant softwood stands comprised primarily of spruce (*Picea glauca* (Moench) Voss, *Picea mariana* (Mill) BSP, and *Picea rubens* Sarg.), eastern hemlock (*Tsuga canadensis* L.) and white pine (*Pinus strobus* L.) (Pinaceae), but which also include some birch (*Betula papyrifera* Marsh and *B. alleghaniensis* Britt.) (Betulaceae), maple (*Acer saccharum* Marsh. and *Acer rubrum* L.) (Aceraceae), American beech (*Fagus grandifolia* Ehrh.) (Fagaceae), and eastern larch (*Larix laricina* (Du Roi) (Pinaceae). Natural disturbances for this type of forest are typically fine-scale fire, wind, diseases, and insects (Loo and Ives 2003). The study sites were located on the private land of Bowater Mersey Paper Company Limited (Fig. 1).

All 11 study sites fell within the Atlantic Interior theme region (Davis and Browne 1996). A closer examination shows that within the Atlantic Interior region, the sites fall within three distinct units. Sites 1-4, 7, and 9-11 are found in the Lake Rossignol

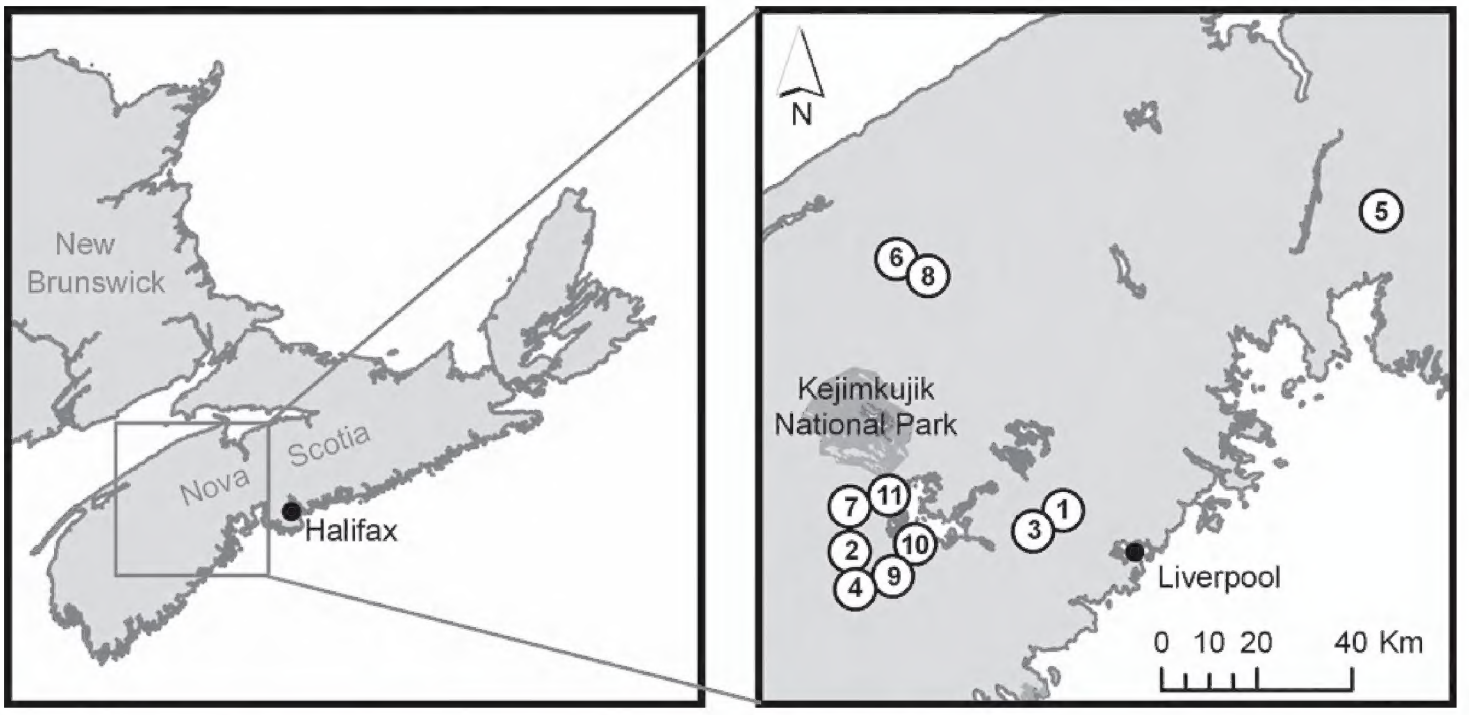

Fig. 1. Map of Bowater Mersey Paper Company Ltd land in Nova Scotia. Bowater Mersey lands highlighted. Site descriptions: 1 & 2 – 40-80 yr, CT; 3 & 4 – 40-80 yr, none; 5 – 80-120 yr, US; 6 & 7 – 80-120, none; 8 – 120+ yr, S; 9 – 120+ yr, S/SH; 10 & 11 – 120+ yr, none.
CT = Commercial thinning; US = Uniform selection harvest; SH = Shelterwood harvest; S = Selection harvest.

sub-unit of the Mersey Meadows unit within the Quarzite Plains district. The Lake Rossignol sub-unit is characterized generally by moderate to coarsely textured soils. The area around the south of Lake Rossignol itself supports eastern hemlock and red spruce, with some shade-tolerant hardwoods such as yellow birch. Culturally, hunting, fishing, and canoeing have been practiced in this area, as the Mersey River was a traditional transport route for the Mi'kmaq and the French. In the 1920s, Lake Rossignol was flooded for hydro power for pulp-and-paper companies, thus affecting the biota and the hunting and fishing of the Mi'kmaq.

Sites 6 and 8 are found in the Alma Lake sub-unit of the Annapolis Drumlins unit within the Drumlins district. The Alma Lake sub-unit is characterized by large granite boulders and well-drained soils. Although these drumlins are made up of granite materials, which are not typical, they do provide very productive forest sites. A mixed forest is common, and include eastern hemlock, red spruce, white pine, sugar maple, yellow birch, as well as some red maple. Tourism is and has been an important activity in this area beginning in the 1870s with American sportsmen who sought out hunting and angling experiences.

Site 5 is found in the South Mountain sub-unit of the Granite Uplands unit within the Granite district. The South Mountain sub-unit is characterized by uniform topographic features, including granite terrain and many large surface boulders. The soil is coarse, well-drained sandy loam, which is usually quite shallow. Characteristic forest trees are red spruce, eastern hemlock, white pine, balsam fir, and red maple with occasional red oak. Fire has played a major role in this area, and regeneration patterns suggest that the area is turning into a coniferous-dominated forest. Forestry activities

are the dominant land use in this largely uninhabited area, but mining and tourism are also prevalent.

Study design

Data collection was replicated in four young (40-80 years) stands, three middle-aged (80-120 years) stands and four old-growth (120+ years) stands. Stand age was determined by coring specimens of the dominant tree species. Within each age class, there were two replicates of each of two treatments, harvested and unharvested, with the exception of the middle-aged stand since it was not possible to find two suitable harvested stands for this age class. Treatment for the harvested stands was by commercial thinning or by removal of approximately 30% of the canopy cover by uniform selection harvest and/or shelterwood harvest. All treated stands had been harvested 3-6 years prior to data collection. During the field season, a thorough overstory analysis was completed for each stand. Measurements including age, species, overstory condition, and diameter at breast height (DBH). Relative density, relative dominance and relative frequency of tree species were then calculated to determine the importance value for each species (Roberts-Pichette and Gillespie 1999).

A quantitative analysis of CWD for each site was completed by Thompson (2004). The sampling techniques used for measurement were adapted from the Nova Scotia Department of Natural Resources Forest Inventory Permanent Sample Plot Field Measurement Methods and Specifications (NSDNR 2002). In each of the sites, five plots of 400 m^2 area were designated randomly for measurement. All snags in each plot were recorded by species, decay class, crown class (intact or broken), height (m) and DBH (cm).

Downed CWD was also measured by census, and for each piece species, diameter at mid-point and length were recorded. Each piece was assigned to one of five decay classes ranging from freshly dead to thoroughly rotted [see Table 5 of Thompson 2004, an adaptation of methods by Sollins (1982)]. Total CWD volumes were calculated and averaged over the five plots to obtain the mean volume per stand.

Beetle sampling methods

Between 15 May 2003 and 11 August 2003, five visits were made to each site approximately two weeks apart. In order to collect as wide a spectrum of species as possible, beetles were sampled using four collection techniques: pitfall traps, Lindgren traps, sweep-netting, and manual searching. Approximately four hours of search time was spent in each site for each of the five visits between 08:00 and 16:00 hr. Timing of visits to the sites was rotational, therefore sites were visited at different times of the day on each date. Collection did not take place during inclement weather, or on mornings following rough weather. An attempt was made to sample as many different sizes and species of vegetation as possible to ensure that a maximum number of habitat types was

examined. Sweeping covered both ground vegetation and tree branches within reach and was performed for approximately one hour per site.

For each site, five pitfall traps were placed and visited five times over the course of the field season. Pitfall traps consisted of plastic cups buried in the ground and covered with a piece of CWD. The traps were filled 1/3 with a solution of one part ethylene glycol and two parts water. One Lindgren trap was set up at each site and was visited four times during the field season. The eight-funnel Lindgren trap was suspended approximately 1.3 m off the ground in a relatively clear area within the site. The Lindgren traps were baited with a solution of half turpentine and half a 70% ethyl-alcohol solution. The collection jar at the bottom of the trap was filled 1/3 with water. Specimens were collected approximately every two weeks and were in good condition and not disarticulated so as to readily allow for identification.

Beetle analysis methods

All the specimens collected in the study were identified to species by C.G. Majka with the assistance of taxonomic experts (listed in the acknowledgements) with the exception of: a) five species of Aleocharinae (Staphylinidae) (5 individuals) for which determination was possible only to the level of genus or tribe; and b) one species of in the genus *Medon* (Staphylinidae: Paederinae) which was identified as *M.* nr. *rufipenne* (Casey, 1905) by Lee Herman. In the case of some beetles in the genera *Cyphon* (Scirtidae: 3 species) and *Atomaria* (Cryptophagidae: 1 species), the species found in the Maritime Provinces are currently under taxonomic revision (Klausnitzer and Majka, and Johnson and Majka respectively). Present determinations of these species may change as a result of these taxonomic revisions. The species of *Paratenetus* (Tenebrionidae) represents an undescribed species currently being described (P. Bouchard and Y. Bousquet, in preparation). The taxonomy and nomenclature employed follows Arnett and Thomas (2000) and Arnett et al. (2002). The collection of Coleoptera has been deposited with the Nova Scotia Museum (NSMC).

The data collected in the present study were additionally analyzed in relation to those gathered by Bishop (1998), a comparable study of the same trophic group of beetles in similar forest environments in Nova Scotia. Saproxylic species (*sensu lato*) were selected according to the criteria specified by Speight (1989), namely species which depend, at some point in their life cycle, on dead or decaying wood, or fungi associated with deadwood, or on other saproxylics. The inclusion of species in this category was made on a specific or, more commonly, generic basis, consulting a wide variety of published sources (commencing with Arnett and Thomas (2000) and Arnett et al. (2002), followed by family-specific treatments such as Larochelle and Larivière (2003)), or if such information was not readily available in the literature, by consulting with appropriate specialists.

Inclusion in the saproxylic category is always accompanied by some degree of uncertainty, particularly in relation to groups or species that have been little investigated

in terms of their bionomics (such as some Elateridae or Aleocharinae). Furthermore, some species, for example large forest-floor predators such as many Carabidae and Staphylininae, while frequently found in or under decomposing wood or logs, and therefore predaceous on other saproxylics, also range widely in the forest floor environment, and consequently may sporadically exit the saproxylic system.

Trophic categories were assigned to all species as a result of information derived from the aforementioned sources. The trophic categories employed were:

Bolitophagous: feeding on the fruiting bodies of fungi (i.e., mushrooms);
Mycetophagous: feeding on fungal hyphae (i.e., mold and mildew feeders);
Myxomycophagous: feeding on slime molds;
Phloeophagous: feeding on phloem of woody vegetation (i.e., cambium feeders);
Phytophagous: feeding on leafy vegetation;
Pollen Feeder: feeding on pollen of vascular plants;
Predaceous: feeding on invertebrates;
Predaceous/Nectarivorous: both predaceous and feeding on nectar;
Rhizophagous: feeding on roots (i.e., plant material growing underground);
Rhizophagous/Predaceous: both rhizophagous and predaceous;
Sap Feeder: feeding on sap;
Saprophagous: feeding on decomposing animal material;
Saprophytic: feeding on decomposing plant material;
Xylophagous: feeding on xylem of woody vegetation.

The categories listed above are general and there are species of Coleoptera that a) overlap between two or more categories, particularly in regard to the different bionomics of adults and larvae; and b) are insufficiently well studied for assignation with acceptable certainty to a particular category. For example, it is not always clear if detritivores are deriving nutrition from decomposing material (i.e., are saprophagous) or from fungal hyphae growing in such a matrix (i.e., are mycetophagous), or a combination of both. Nonetheless, such categorizations are a useful first-order approximation to gain insight into the trophic structure of forest-beetle communities.

Beetle data analysis: statistical techniques

The sampling methods of this study emphasized alpha diversity (species richness). For the purpose of analysis, all species collected, no matter the quantity, were only counted as present or absent in any given site. A two-way analysis of variance (ANOVA) was performed based on species richness (sum of species) because it allows the investigation of interactions. An ANOVA was performed for both age and harvest treatment. To facilitate comparison with the present study, the data from Bishop (1998) (which included quantitative abundance information) were converted to presence/absence data. All subsequent data treatments were identical for both studies.

To analyse the differences in species composition between sites, a SIMPER (similarity percentages) test (Clarke and Warwick 2001) was completed. This test was used

to determine which species, from all dates in each site, contributed most to the dissimilarity between sites; those species that provided the strongest discrimination between two sites. The species selected for the modified list were those whose similarity/dissimilarity, divided by the standard deviation, had a value greater than or equal to 1. All subsequent tests were performed using the modified species list.

The presence/absence of all species over all dates in each site was used to calculate the Bray-Curtis similarity measure. A one-way analysis of similarities (ANOSIM) between samples was performed for the factors of age and treatment within each site using the Bray-Curtis similarity measure (Clarke and Warwick 2001). Given the qualitative, presence/absence nature of the data collected, the SIMPER analysis was most applicable. ANOSIM was used for variables such as species richness and trophic category richness (trophic composition). Multi-dimensional scaling (MDS) plots were completed for each of the variables. The MDS plots give a two-dimensional ordination, illustrating relationships between sites.

A test of taxonomic distinctiveness (TAXD) was performed using the following taxonomic levels: species, genus, tribe, subfamily, family, superfamily, series, and suborder. The TAXD measures biodiversity based on the relatedness of species within a sample, thus adding additional statistical sampling properties (Clarke and Warwick 2001).

No standardisation or transformation was performed before analysis. Several qualitative comparisons were made between the two studies, including total number of species, differences in species origin, and trophic categories. A quantitative comparison of species richness between the two studies with differing species and specimen numbers was possible using the EstimateS rarefaction curve (Colwell 2004).

Relationships between beetle communities and CWD

Coarse woody debris volumes were calculated by Thompson (2004) using only pieces where diameter > 7.0 cm. Stand volumes were analyzed with respect to stand age and harvest treatment using a general linear model (GLM) in SPSS 11.5 (SPSS 2002). The effects of age, treatment, and age and treatment combined were tested for their influence on the volume of CWD in each stand. Decay class and CWD diameter across age groups and harvest treatment were plotted to look for trends in the data.

The multivariate patterns arising from the CWD data were compared to those of beetle species data to determine the extent to which CWD affects beetle species diversity. Both an analysis of covariance (ANCOVA) and a correlation analysis were used to test whether CWD volumes were correlated with beetle species richness (Clarke and Warwick 2001).

CWD volume data were then used to assign each stand to one of three volume classes: 1-55 m^3/ha (low), 56-110 m^3/ha (medium) and 111-165 m^3/ha (high). The CWD volume classes were paired with beetle data. CWD was qualified as a factor and analyzed using ANOSIM.

Results

Overview of stand data

The eleven study sites were mainly dominated by red spruce, white pine, and/or eastern hemlock (Fig. 2), ranging in age from 49 years to approximately 160 years (Table 1). Minimum mean diameter at breast height (DBH) was 10.5 cm at site 4 and maximum mean DBH was 24.6 cm at site 10. The mean DBH of dominant species ranged from 10.8 cm for the red spruce, white pine, and balsam fir in site 4, to 28.4 cm for the eastern hemlock and red spruce in site 10. Stand density ranged from 510 stems/ha in site 9 to 4,320 stems/ha in site 4.

Using data collected by Thompson (2004), volume of CWD for each decay class was plotted for each of the 11 forest stands. Volumes of CWD varied from > 160 m^3/ha to < 40 m^3/ha. CWD total volumes were clearly higher in the oldest stands sampled (Fig. 3). Tree species composition also varied across the sites (Fig. 4), but with no clear pattern associated with stand age or treatment. Site 5 in particular had a large proportion of red maple, and site 8 had a large proportion of eastern hemlock. Sites 1, 2, 4, and 7 have no white birch CWD.

Table 1. Summary of characteristics of eleven study sites on Bowater land in southwestern Nova Scotia including mean age, mean height, mean diameter at breast height (DBH), dominant species and density.

Site	Harvest treatment[1]	Dominant overstory species[2]	Age class (years)	Mean Age (years)[3]	Total Basal Area (m^2/ha)	Mean Height (m)	Mean DBH (cm)	Mean DBH of Dominant Species (cm)	Density (stems/ha)
1	CT	rS	40-80	67	38.4	18.7	12.9	14.4	2055
2	CT	wP/rS	40-80	59	35.6	20.9	18.2	20.0	1080
3	None	rS/eH	40-80	58	45.3	19.0	14.7	11.5	1930
4	None	rS/wP-bF	40-80	55	46.4	15.9	10.5	10.8	4320
5	US	rS	80-120	100	26.7	20.0	13.9	16.6	1220
6	None	rS/wP	80-120	95	37.6	19.0	15.1	20.4	1410
7	None	rS	80-120	90	52.3	21.3	18.3	17.8	1405
8	S	eH/rS	120+	ca. 160	39.4	20.6	16.5	21.3	1050
9	S/Sh	eH/rS	120+	126	34.9	25.8	22.2	22.8	510
10	None	eH/rS	120+	190	57.8	25.5	24.6	28.4	895
11	None	eH/rS	120+	190	47.1	25.0	20.3	20.5	1105

[1] CT = Commercial thinning; US = Uniform selection harvest; Sh = Shelterwood harvest; S = Selection harvest.

[2] rS = red spruce; wP = white pine; eH = eastern hemlock; bF = balsam fir

[3] Age determined by cores of dominant tree species.

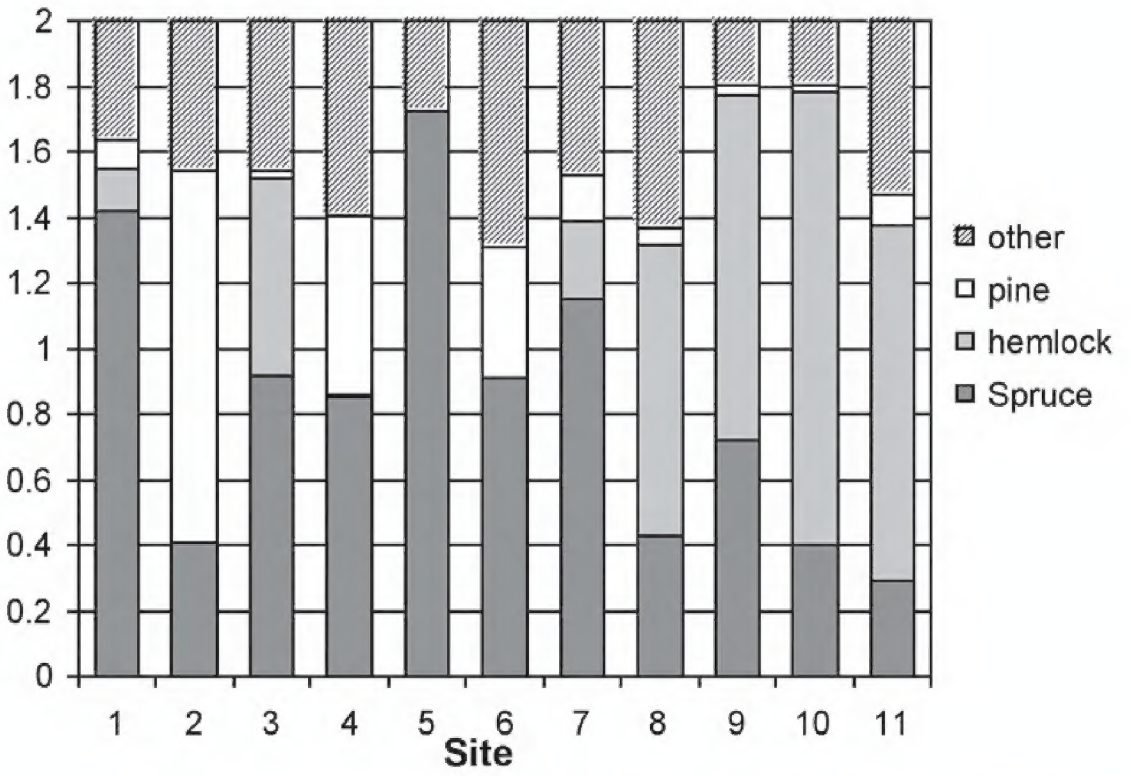

Fig. 2. Overstory composition for dominant tree species based on importance value (Importance Value = Relative Density + Relative Dominance + Relative Frequency). Site descriptions: 1 & 2 – 40-80 yr, CT; 3 & 4 – 40-80 yr, none; 5 – 80-120 yr, US; 6 & 7 – 80-120, none; 8 – 120+ yr, S; 9 – 120+ yr, S/SH; 10 & 11 – 120+ yr, none.
CT = Commercial thinning; US = Uniform selection harvest; SH = Shelterwood harvest; S = Selection harvest.

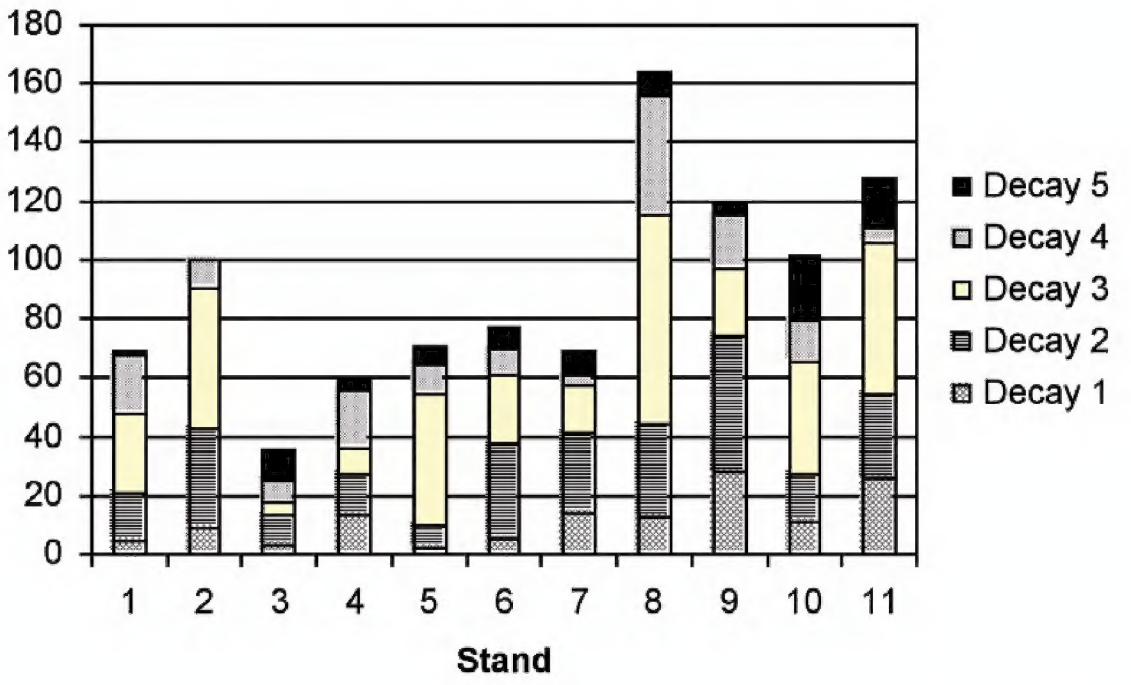

Fig. 3. Volume of coarse woody debris (CWD) by decay class for 11 stands in southwestern Nova Scotia as measured by Thompson (2004). Decay classes are summarized as follows: "1" is freshly dead, little to no rot; in "2", the bole is mostly sound; "3" has well-established rot and significant bark loss; "4" is advanced decay; and "5" is rotted through but still of wood character. Site descriptions: 1 & 2 – 40-80 yr, CT; 3 & 4 – 40-80 yr, none; 5 – 80-120 yr, US; 6 & 7 – 80-120, none; 8 – 120+ yr, S; 9 – 120+ yr, S/SH; 10 & 11 – 120+ yr, none.
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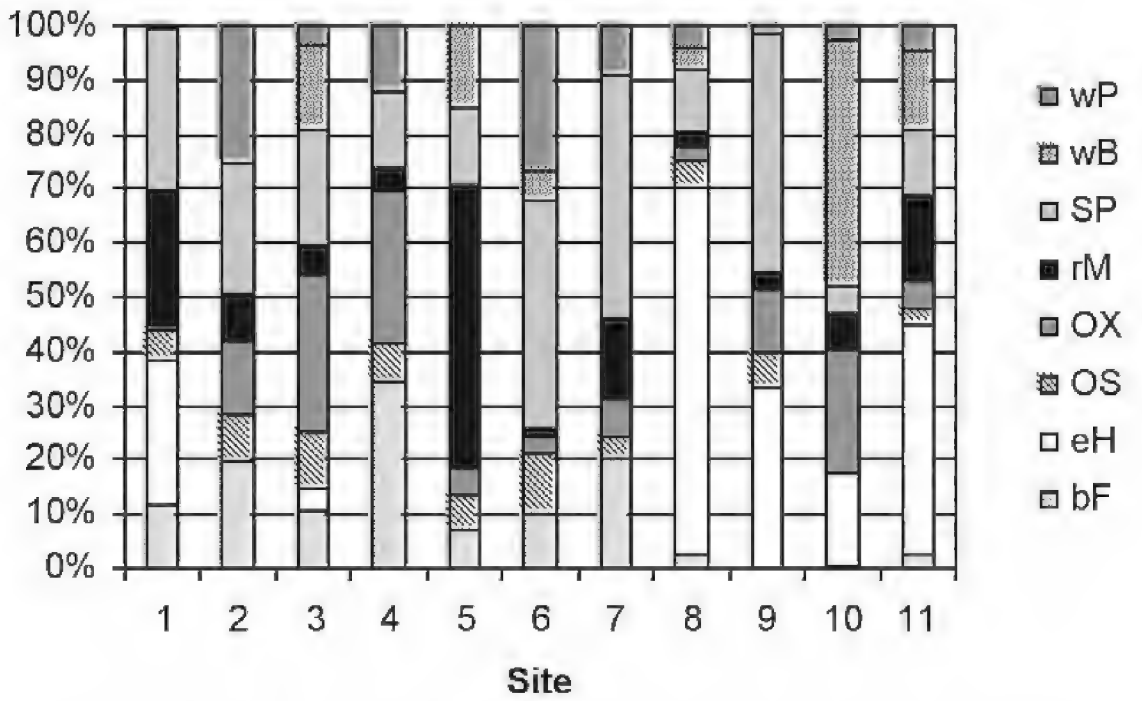

Fig. 4. Percentage of coarse woody debris (CWD) volume by tree species for 11 stands in southwestern Nova Scotia (Thompson 2004). Tree species: wP White Pine; wB White Birch; SP Spruce spp.; rM Red Maple; OX unidentified hardwood; OS unidentified softwood; eH Eastern Hemlock; bF Balsam Fir. Site descriptions: 1 & 2 – 40-80 yr, CT; 3 & 4 – 40-80 yr, none; 5 – 80-120 yr, US; 6 & 7 – 80-120, none; 8 – 120+ yr, S; 9 – 120+ yr, S/SH; 10 & 11 – 120+ yr, none.
CT = Commercial thinning; US = Uniform selection harvest; SH = Shelterwood harvest; S = Selection harvest.

Overview of beetle data

Beetle sampling yielded 2,302 specimens of 346 species from 56 families (Appendix 1). Of the 346 beetle species, 264 were determined to be either facultative or obligatory saproxylics. Fifteen species (4%) were common to all young stands, 25 species (7%) were common to all medium-aged stands, and 16 species (5%) were common to all old stands. Eleven species (3%) were common to all harvested stands and seven species (2%) were common to all unharvested stands. Fifty-one species were caught in only one of the 11 sampling sites. Only three species (*Isomira quadristriata* (Couper), *Platydracus viridanus* (Horn) and *Rhagonycha mandibularis* (Kirby)) were common to all 11 sites.

Results from the SIMPER analysis identified 97 beetles primarily accounting for species assemblage similarities and dissimilarities for factors of age and treatment. These species were used for all subsequent analyses. In comparison, 387 species were collected by Bishop (1998), 76 of which were primarily responsible for species assemblage similarities and dissimilarities and were used in subsequent analysis.

Comparative analysis of beetle communities

Both the present study and Bishop (1998) found relatively similar numbers of beetle species (346 and 387 respectively). However, Bishop (1998) collected over four times the number of specimens collected in the present study (9,881 vs. 2,301 respectively).

The larger number of individuals in Bishop's (1998) study reflects a greater sampling effort (180 flight intercept traps which were continuously in place for 90 days during the spring/summer field season). Similar numbers of beetle species were considered facultative or obligatory saproxylics (264 species in the present study; 297 in Bishop (1998)). One hundred and sixty-four species were common to both studies. Results from a rarefaction analysis (Fig. 5) indicate that, if similar numbers of specimens were collected in the Bishop (1998) study, the number of beetle species would not have been as high as in the present study (Fig. 5). It is also clear that the number of species in the present study has not yet approached an asymptote (Fig. 5). This indicates that the four collecting techniques we employed are sampling a much wider spectrum of the forest beetle community than the single technique employed by Bishop (1998).

For example the present found more species of forest floor beetles in the families Carabidae, Tenebrionidae, and Histeridae than did Bishop (1998) (Fig. 6). Although some of these species are macropterous and are capable of flight, it would appear that many of them fly infrequently. The larger numbers of Curculionidae (Fig. 6) in the present study consist almost entirely of flightless species in the subfamily Entiminae, which are not sampled at all by flight intercept traps. The present study also collected substantial numbers of specimens in the Geotrupidae (*Geotrupes horni* Blanchard, a forest floor species) and Zopheridae (*Phellopsis obcordata* (Kirby), a largely flightless bolitophagous species found on polypore fungi) (Appendix 1), two families not represented in the material collected by Bishop (1998).

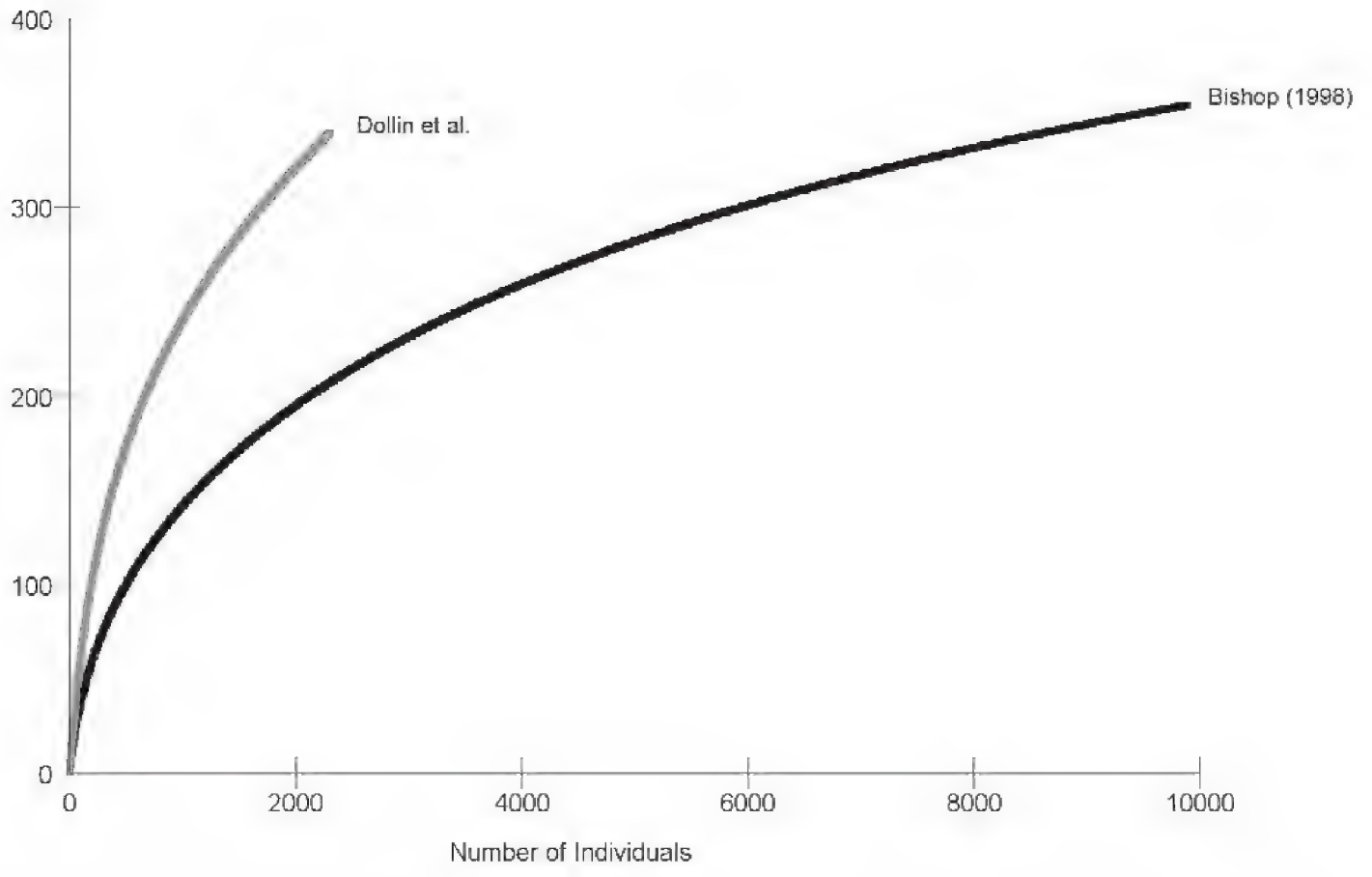

Fig. 5. Rarefaction curve demonstrating projected species richness for number of individuals based on Bishop (1998), and the present study (Dollin et al.) beetle collections.

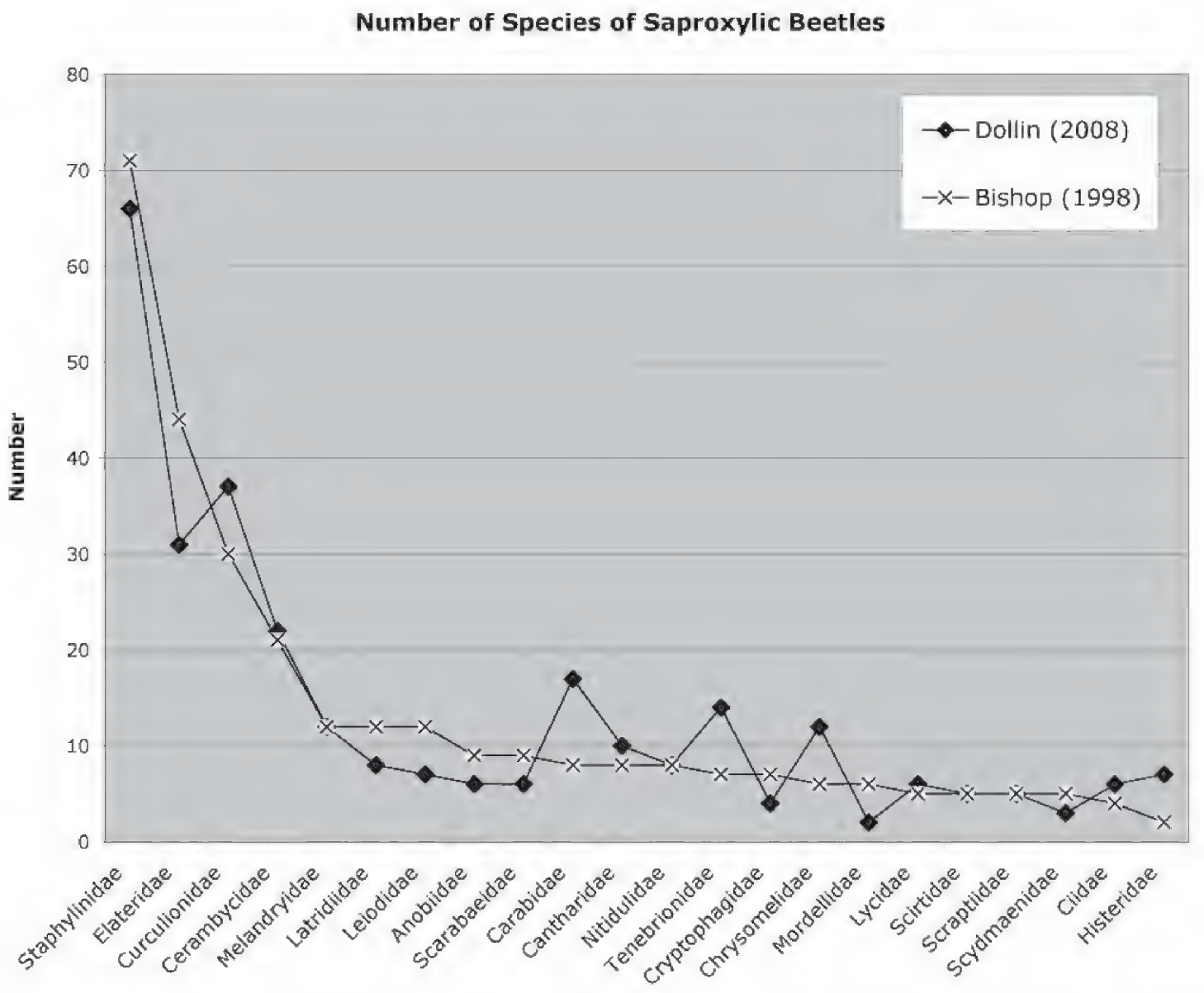

Fig. 6. The number of species of beetles in the 22 most speciose families collected in the present study and in Bishop (1998).

A sizeable number of species were restricted to stands of specific ages: 47 were exclusively found in young stands, 52 species were found only in middle-aged stands and 69 species were exclusively found in old stands. These 69 species are listed in Table 2 along with indications of their abundance and distribution within Nova Scotia. While such categorizations admittedly include a degree of subjective judgment, and are based on a continually evolving base of knowledge of the Coleoptera in the province, they do allow a mechanism for selecting potentially vulnerable species. They include 23 rarely collected and locally distributed species in Nova Scotia (indicated in boldface in Table 2) that may be indicator species of old-growth forests conditions.

Effects of stand age

More species were present in middle-aged and old stands than in young stands ($F = 22.511$; d.f. = 2; $p = 0.003$). Significantly more species were present in middle-aged and old stands than in young stands (Fig. 7).

Table 2. Coleoptera found only in old-growth (120+ years) forests

Family	Species	Abundance	Distribution	Saproxylic	Reference
Carabidae	***Gastrellarius honestus* (Say)**	rare	local	SX	Majka et al. (2007b)
	Harpalus affinis Schrank †	abundant	widespread		Majka et al. (2007b)
Histeridae	*Platysoma coarctatum* LeConte	uncommon	scattered	SX	Majka (2008a)
Leiodidae	***Agathidium oniscoides* Beauvois**	rare	local	SX	unpublished data
	Sciodrepoides terminans (LeConte)	abundant	widespread		unpublished data
Scydmaenidae	***Stenichus badipes* (Casey)**	rare	local	SX	unpublished data
Staphylinidae	***Phloeonomus laesicollis* (Mäklin)**	rare	local	SX	unpublished data
	***Phloeostiba lapponicus* (Zetterstedt)** *	rare	local		unpublished data
	Bibloporus bicanalis (Casey)	common	widespread	SX	unpublished data
	***Pycnoplectus linearis* (LeConte)**	rare	local	SX	unpublished data
	Batrisodes lineaticollis (Aubé)	uncommon	widespread	SX	unpublished data
	Tachinus basalis Erichson *	uncommon	widespread	SX	Campbell (1973)
	Oxypoda amica Casey	common	local	SX	Klimaszewski et al. (2006)
	***Gyrophaena sculptipennis* Casey**	rare	local	SX	unpublished data
	Aleocharine species 4				
	Anaquedius vernix (LeConte)	uncommon	widespread	SX	Smetana (1971)
	Quedius canadensis (Casey)	uncommon	widespread	SX	Smetana (1971)
	***Quedius densiventris* (Casey)**	rare	local	SX	Smetana (1971)
	Gabrius picipennis (Mäklin)	abundant	widespread	SX	Smetana (1995)
Scarabaeidae	*Dialytes striatulus* (Say)	common	widespread		unpublished data
	Dichelonyx albicollis (Burmeister)	common	widespread	SX	unpublished data
	Dichelonyx subvittata (LeConte)	common	widespread	SX	unpublished data
	Osmoderma scabra Beauvois	common	widespread	SX	unpublished data
Buprestidae	*Dicerca punctulata* (Schönherr)	common	widespread	SX	Bright (1987)
Elateridae	*Dalopius fuscipes* Brown	uncommon	widespread	SX	Majka & Johnson (2008)
	***Ampedus protervus* (LeConte)**	rare	local	SX	Majka & Johnson (2008)

Family	Species	Abundance	Distribution	Saproxylic	Reference
	Melanotus similis (Kirby)	common	widespread		Majka & Johnson (2008)
	Liotrichus vulneratus (LeConte)	uncommon	widespread	SX	Majka & Johnson (2008)
	Neohypdonus tumescens (LeConte)	uncommon	widespread	SX	Majka & Johnson (2008)
Lycidae	***Lopheros fraternus* (Randall)**	rare	local	SX	unpublished data
	***Plateros bispiculatus* Green**	rare	local	SX	unpublished data
Cantharidae	*Cantharis rotundicollis* Say	common	widespread		unpublished data
	***Atlantycha bilineata* Say**	rare	local		unpublished data
	Podabrus modestus (Say)	uncommon	scattered		unpublished data
Anobiidae	*Microbregma emarginatum* (Duftschmid) †	common	widespread	SX	Majka (2007a)
	***Dorcatoma falli* White**	rare	local	SX	Majka (2007a)
Nitidulidae	*Colopterus truncatus* (Randall)	common	widespread	SX	Majka & Cline (2006a)
Monotomidae	***Rhizophagus remotus* LeConte**	rare	local	SX	unpublished data
Silvanidae	*Silvanus bidentatus* (Fabricius) †	common	widespread	SX	Majka (2008b)
Cucujidae	*Cucujus clavipes* Fabricius	uncommon	widespread	SX	Majka (2008b)
Laemophloeidae	*Laemophloeus biguttatus* (Say)	uncommon	widespread	SX	Majka (2008b)
Cryptophagidae	*Atomaria ephippiata* Zimmerman	uncommon	widespread	SX	unpublished data
Coccinellidae	*Scymnus lacustris* LeConte	uncommon	widespread		Majka & McCorquodale (2006)
Mycetophagidae	***Mycetophagus serrulatus* Casey**	rare	local	SX	unpublished data
Ciidae	***Ceracis sallei* Mellié**	rare	local	SX	Majka (2007c)
Tetratomidae	*Penthe pimelia* (Fabricius)	uncommon	widespread	SX	Majka & Pollock (2006)
Melandryidae	*Dircaea liturata* (LeConte)	uncommon	widespread	SX	Majka & Pollock (2006)
Mordellidae	*Mordellistena fuscipennis* (Melsheimer)	common	widespread		Majka & Jackman (2006)
Colydiidae	***Lasconotus borealis* Horn**	rare	local	SX	Majka et al. (2006)
Tenebrionidae	***Neomida bicornis* (Fabricius)**	rare	local	SX	Majka et al. (in press)
	Scaphidema aeneolum (LeConte)	common	widespread	SX	Majka et al. (in press)
	Iphthiminus opacus (LeConte)	uncommon	widespread	SX	Majka et al. (in press)

Family	Species	Abundance	Distribution	Saproxylic	Reference
Pyrochroidae	*Dendroides canadensis* Latreille	uncommon	widespread	SX	Majka (2006a)
Cerambycidae	*Pidonia ruficollis* (Say)	common	widespread	SX	unpublished data
	***Pygoleptura nigrella* (Say)**	rare	local	SX	unpublished data
	***Sachalinobia rugipennis* (Newman)**	rare	local	SX	unpublished data
	Stictoleptura canadensis (Olivier)	common	widespread	SX	unpublished data
Chrysomelidae	***Paria fragariae kirki* Balsbaugh**	rare	local		unpublished data
Curculionidae	*Otiorhynchus sulcatus* (Fabricius) †	abundant	widespread		Majka et al. (2007a)
	Polydrusus impressifrons (Gyllenhal) †	uncommon	local		Majka et al. (2007a)
	***Conotrachelus posticatus* Boheman**	rare	local		Majka et al. (2007a)
	Pissodes strobi (Peck)	common	widespread		Majka et al. (2007a)
	Hylurgops rugipennis pinifex (Fitch)	common	widespread	SX	Majka et al. (2007a)
	Dendroctonus simplex LeConte	uncommon	local	SX	Majka et al. (2007a)
	Dendroctonus valens LeConte	common	widespread	SX	Majka et al. (2007a)
	Pityokteines sparsus (LeConte)	common	widespread	SX	Majka et al. (2007a)
	Orthotomicus caelatus (Eichhoff)	common	widespread	SX	Majka et al. (2007a)
	***Pityophthorus cariniceps* LeConte**	rare	local	SX	Majka et al. (2007a)
	Monarthrum mali (Fitch)	common	widespread	SX	Majka et al. (2007a)

Abundance Categories (reflective of collection frequency): abundant, common, uncommon, rare. Distribution categories: widespread, scattered, local. Saproxylic Status: SX, saproxylic species; no entry, non-saproxylic species.

†, adventive Palaearctic species; *, Holarctic species; no symbol, Nearctic species. Entries highlighted in boldface represent rarely collected local species, possibly indicative of old-growth forest conditions.

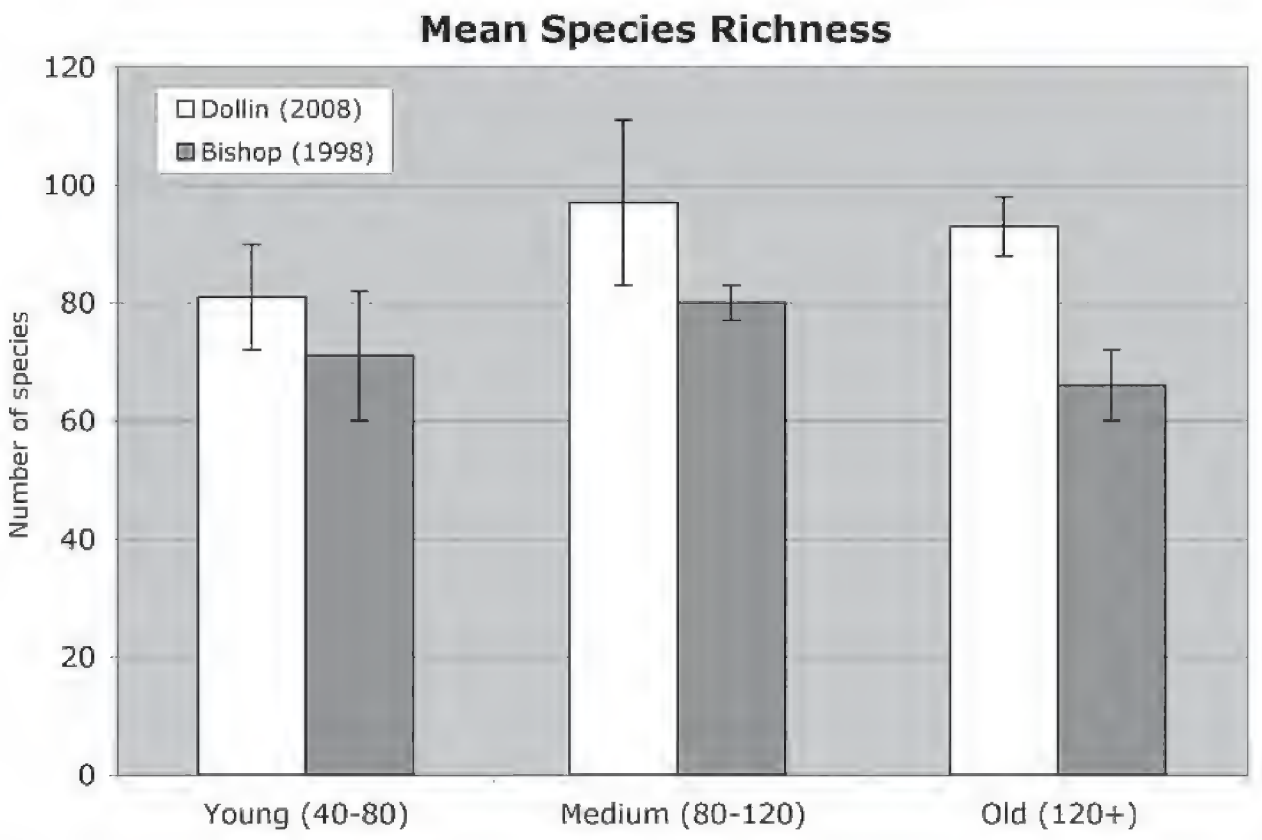

Fig. 7. Mean species richness of beetles in different forest stand age classes, including standard deviation from both the present study and Bishop (1998).

Species composition was significantly affected by stand age. The Global R, ANOSIM was 0.442 with a significance level of 0.7% (the sample statistic is similar to, yet not synonymous with, a p-value of 0.007). Both the young and mid-aged stands were significantly different from the old stands, but there was no significant difference between the young and mid-aged stands. Stand age had a pronounced effect on species composition.

Trophic composition was also affected by stand age (Global R, ANOSIM of 0.503 with a significance level of 0.1%). There were significant differences in the trophic composition of beetle communities between young and both mid-aged and old groups, but not between mid-aged and old groups.

The TAXD test did not show any significant results for age, therefore indicating that there were no differences detected in the taxonomic distinctiveness of species between age groups of stands.

Comparative effects of stand age

Species richness was affected by stand age in this study only. Young unharvested stands had the lowest species richness, and mid-aged harvested stands the highest. All other stand age-treatment combinations had similar species richness. Stand age had no significant effect ($F = 1.632431$; d.f. = 2; $p = 0.217$) on species richness in Bishop (1998). Species composition and trophic composition were significantly affected by stand age only in the present study.

Effects of harvest treatment

Species richness was affected by treatment type. The mean number of species present in harvested sites was significantly higher than in unharvested sites (F = 13.395; d.f. = 1; p = 0.015) (Fig. 8). The interaction between harvest treatment and age was not significant. Species composition was significantly affected by harvest treatment (Global R, ANOSIM of 0.299 with a significance level of 3.7%). Treatment did have a pronounced effect on species composition.

Species trophic composition was not significantly affected by harvest treatment (Global R, ANOSIM of 0.155 with a significance level of 13.4%). The difference was not statistically significant. The TAXD test did not show any results for harvest treatment, thereby indicating that there was no difference in the taxonomic distinctiveness of species between harvested and unharvested sites.

Comparative effects of harvest treatment

Species richness was affected by treatment type in this study only. Harvest treatment had no effect on species richness in Bishop (1998). Species composition was significantly affected by harvest treatment in Bishop (1998) (Global R, ANOSIM of 0.254 with a significance level of 0.1%). Treatment thus had a pronounced effect on species composition. Species trophic composition was not significantly affected by harvest treatment in Bishop (1998).

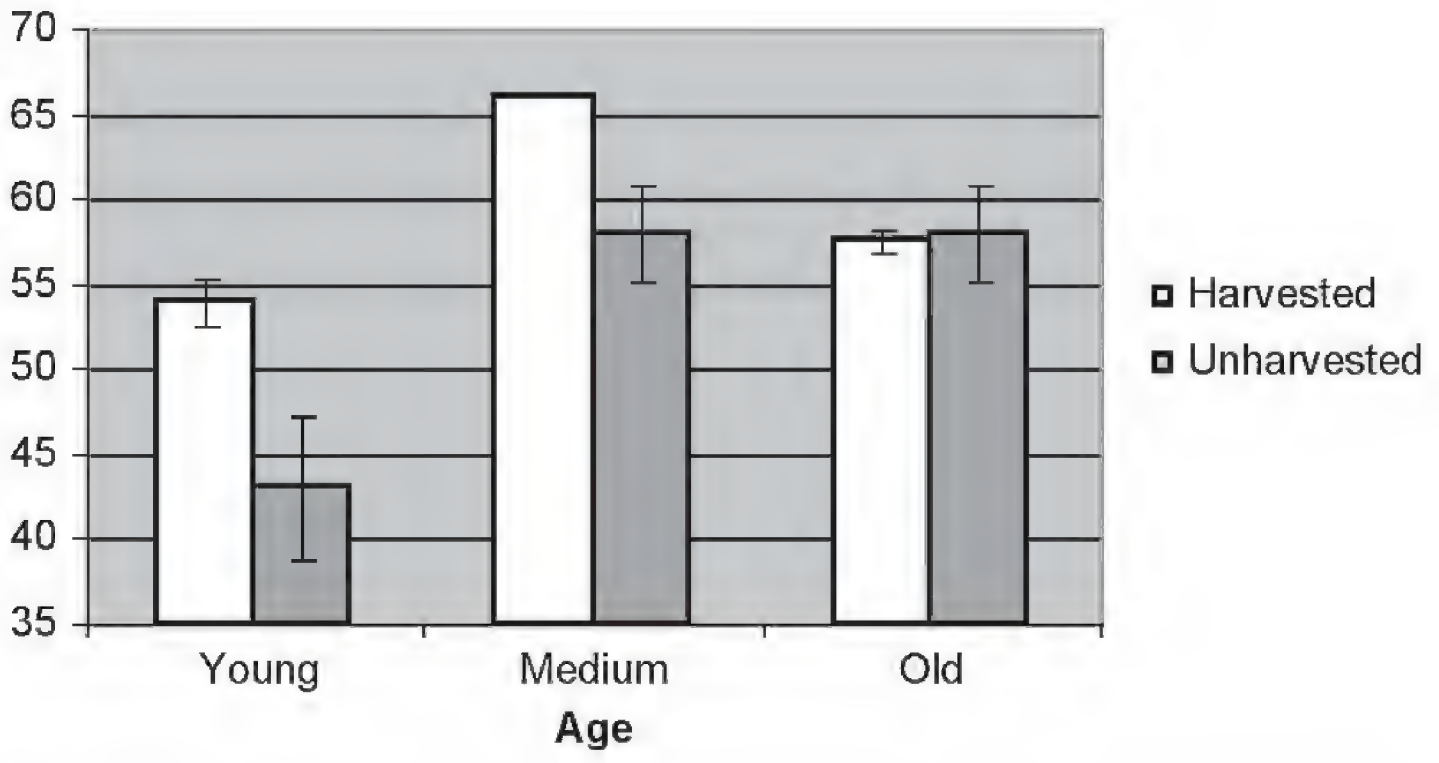

Fig. 8. Mean species richness across harvest treatment, including standard deviation, for 11 stands in southwestern Nova Scotia.

Analysis of relationships

There is a weak positive relationship between volume of CWD and species richness (Fig. 9). An increase in CWD volume is accompanied by an increase in beetle species richness, but the relationship is not statistically significant ($F = 2.48$; d.f. = 9; $p = 0.15$).

Species composition was not affected by volume of CWD. This is true even with the use of the modified species list developed through the SIMPER analysis. The Global R, ANOSIM value was 0.234 ($p = 0.086$). The greatest difference was seen between the group with the lowest volume of CWD (1-55 m3/ha) and the group with the highest volume of CWD (111-165 m3/ha) ($R = 0.75$, $p = 0.10$).

Discussion

Beetle Sampling Methods

The methods used to collect beetles in the present study were quite different from those employed by Bishop (1998). Flight intercept traps (FITs), employed by the latter study, were more easily standardized. The use of FITs is much less laborious in the field compared to manual searching (Siitonen 1994). As well, there is ongoing collection even when the researcher is not present. There are several shortcomings associated with the use of FITs or other passive collection methods. Some species or even families of beetles live inside decaying trunks for several generations and would therefore not likely be caught in flight (Siitonen 1994). Given the common trend of abundance of large, poorly dispersing specialists to decrease with increasing disturbance, and like-

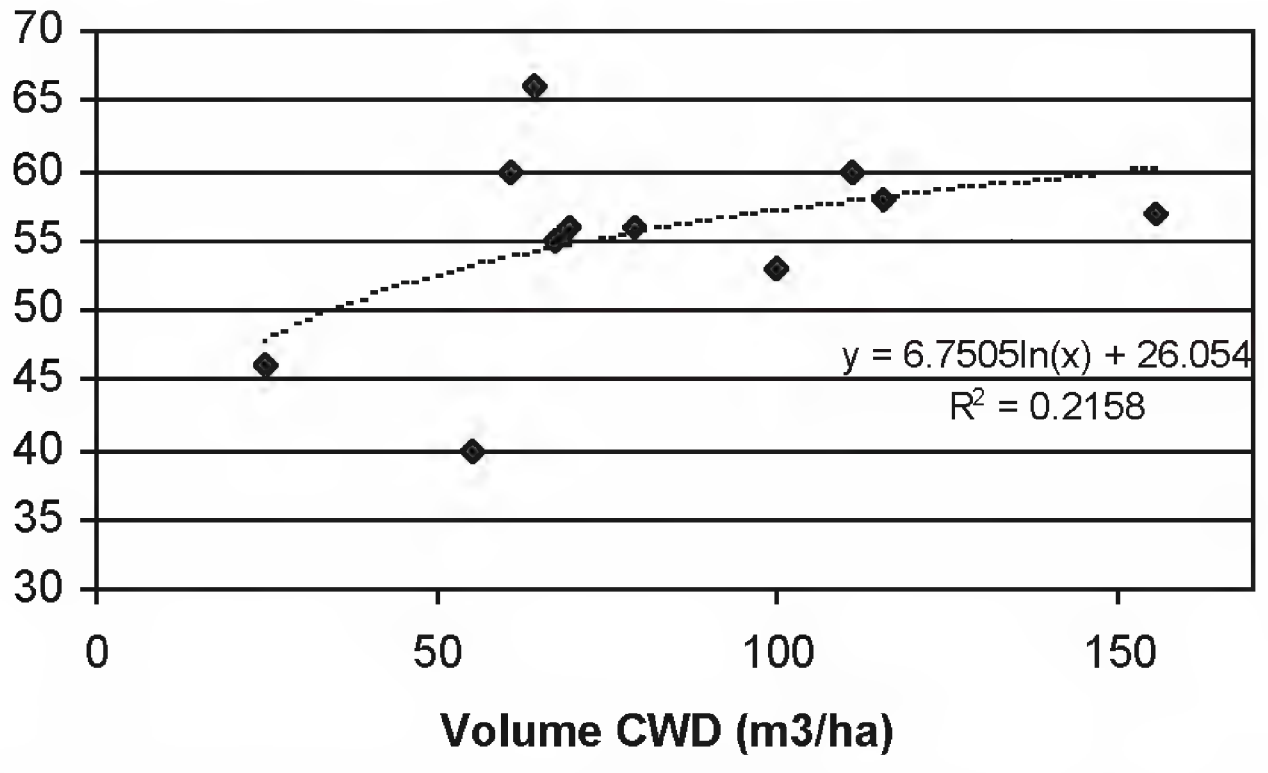

Fig. 9. Scatter plot demonstrating a non-significant positive correlation between beetle species richness and CWD volume. Included are the regression equation and the R^2 value.

wise for small generalists to increase in abundance, the bias of FITs may be significant (Rainio and Niemela 2003). If the presence of specialists goes undetected in disturbed forest ecosystems, an incorrect picture of beetle diversity would emerge for those sites. Additionally, of course, flightless species are not collected at all.

In studies conducted in the Oulanka National Park region of Finland (an area whose beetle fauna is very thoroughly documented) Muona (1999) found that FITs caught 44-48.3% of forest beetle species. A combination of pitfall traps and FITs caught 60.5% of species, and pitfall traps, FITs, and sweep nets taken together collected 91.4% of species. Only 55% of rare species were caught and only 25% of species designated as threatened were collected. Muona (1999) pointed out that the populations of many rare species are small and they may be patchily distributed, making them difficult to detect and sample.

Martikainen and Kouki (2003) found that window traps were the most effective trap type in sampling threatened beetles. However, rarer species were not collected using any other method besides direct searching. Direct searching includes netting, peeling of bark, and other searching methods for beetles by entomologists themselves. As well, the efficacy of the window traps depended largely on the location of the trap, and those located randomly were not as effective.

Manual searching is a more time-intensive process than passive methods like FITs, but the time saved by the latter approach has to be balanced against the time involved in subsequent sorting, pinning, and identification. In the Bishop (1998) study, 4.3 times the number of specimens had to be processed. In designing sampling programs for environmental impact assessment or ecological monitoring in a fiscal climate when both human and financial resources may be limited, such considerations may also have an important bearing on decision-making (Oliver and Beattie 1996b).

Although alpha diversity (species richness) carries less information than quantitative species abundance, it can be less time- and labour-intensive to collect and process such information. Competitive exclusion (*sensu* Hardin 1960) supports the view that measuring alpha diversity is indicative of the presence or absence of microhabitats occupied by respective species. Hence, examining species richness, particularly of hyper-diverse groups such as Coleoptera, allows for an examination of some dimensions of the environment as perceived through a fine ecological mesh (Majka and Bondrup-Nielsen 2006).

Although the number of specimens collected varied considerably between the two studies (2,302 specimens in the present study, and 9,881 by Bishop (1998)), the total number of beetle species was rather similar (346 versus 387, respectively). Rarefaction analysis (Fig. 5) indicates that the expected number of species collected in the present study would be much lower. This higher-than-expected species richness may be a function of using four collection methods as compared with one by Bishop (1998). It is possible that the combination of four collection methods was efficient in sampling many microhabitats and avoiding the collection of high numbers of specimens of the same species. It has been suggested that to maximally sample the species present in a particular environment, several trapping methods should be employed (Økland 1996; Ranius and Jansson 2002; Martikainen and Kouki 2003).

Beetle communities

Beetle communities were similar in both studies in terms of species richness, and proportions of species from different zoogeographic origins (Nearctic, Holarctic, adventive Palaearctic). These similarities support the contention that both approaches are sound with respect to producing accurate (albeit incomplete) representations of forest beetle communities. Not all groups of beetles are thoroughly sampled by either of these approaches. For instance, both studies recorded few species of Buprestidae, even though 39 species of these saproxylic beetles have been recorded in Nova Scotia (C.G. Majka, unpublished data), and some forest-litter species such as those in the Ptiliidae were poorly represented in both studies since litter sifting was not a technique employed in either. Surprisingly, macropterous, litter-dwelling species in the Pselaphinae and Scydmaenidae were well represented in both studies (collected by flight-intercept and funnel traps) (Appendix 1).

Furthermore the combination of techniques employed in the present study better samples forest floor species in the Carabidae, Tenebrionidae, Entiminae, Geotrupidae, and Zopheridae than flight-intercept traps do (Fig. 6). Nevertheless, these approaches, while offering an incomplete representation of forest beetle communities, do provide an apparently consistent index of these communities, something of utility in terms of comparing forests of different ages and compositions, and also in monitoring changes in forest communities over time.

Martikainen and Kouki (2003) suggested that the measurement of the number of species has several advantages compared to other estimates. Advantages include availability and/or ease of measurement and consistency over large geographic areas. They also indicated that the number of trapped species should be over 300-400, corresponding to a number greater than 4,000 individuals, in order to include rare species (Martikainen and Kouki 2003).

The proportion of introduced species of beetles in an environment can frequently be an indicator of disturbance, with anthropogenic or disturbed habitats typically exhibiting much higher proportions of adventive species (Spence and Spence 1988). In the present study, 22 of 346 saproxylic species (6.4%) were introduced, while in Bishop's (1998) work, 20 of 387 species (5.2%) were introduced. In contrast, in a study of Coleoptera of Point Pleasant Park, Nova Scotia, a highly disturbed early successional forest, C.G. Majka found 17.7% of species to be introduced (unpublished data). This compares to the Nova Scotia provincial fauna as a whole which consists of 15.3% of introduced species (C.G. Majka, unpublished data).

The number of species previously unrecorded for Nova Scotia in both studies indicates that knowledge of the baseline biodiversity of saproxylic beetles in Nova Scotia is far from complete. The present study found 135 species of beetles unrecorded from Nova Scotia by Bousquet (1991). Both studies thus contribute to ongoing programs to document the distribution, abundance, origins, and trophic categories of the beetle fauna of the province which are essential for many ecological, zoogeographic, and environmental monitoring studies (McCorquodale et al. 2005). Some specimens derived

from this study have already contributed to recent surveys of the Coleoptera fauna of the region (Bousquet and Laplante 2006; Majka 2006a, 2006b, 2007a, 2007b, 2007c, 2008a; Majka and Cline 2006a, 2006b; Majka and Johnson 2008; Majka and Pollock 2006; Majka et al. 2006, 2007a, 2007a, in press).

Stand age

In the present study, stand age was shown to affect both species richness as well as species composition. This agrees with other studies in both Canada and Europe (Kaila et al. 1997, Hammond et al. 2004). In general, as stand age increases, so does species richness. This high level of beetle species richness in old forests is likely related to habitat heterogeneity, often characteristic of old-growth forests (Heinrichs 1983). Old-growth forests typically are more structurally diverse, and have higher concentrations of large-diameter CWD, therefore supporting a wider array of microhabitats suitable for a larger diversity of species (Duchesne 1994). In both the present study and in Bishop (1998) old stands had a lower species richness then medium-aged stands (Fig. 7). Indeed in Bishop (1998) the old stands had a slightly lower species richness than young stands (Fig. 7). These results are counterintuitive. Further investigations should be undertaken in similar northern-temperate forests with extensive disturbance histories to ascertain if the present results are anomalous, or if there are reasons why the species-richness in older forest stands is being underestimated and inadequately sampled by present collection techniques (see the further discussion on this subject in the section below).

Species assemblages of beetles of younger stands do not appear to be entirely similar to those present in older forest stands. Not only were species compositions different, but the trophic category compositions also varied slightly between young and old stands. This may be due to differences in decay class and diameter class of the CWD, and therefore to differences in food and habitat availability present in the different-aged forest stands. A study by Hammond et al. (2004) saw an increase in trophic complexity in older stands.

Harvest treatment

Harvest treatment was shown to affect both beetle species richness and composition. The results from this study diverge from many other studies in that species diversity was higher in the partially harvested sites than in the unharvested sites. Kaila et al. (1997) found that median numbers of species caught did not differ between closed forests and clearcuts, but species assemblages varied greatly. In other European studies, such as those by Økland et al. (1996) and Simila et al. (2003), species richness was significantly higher in semi-natural or unharvested forests than in managed forests. Managed forests in the Scandinavian setting are, however, quite different than those in

Canada (Kimmins 1997). However, a Canadian study by Klimaszewski et al. (2003) measured arthropod abundance and found that clearcut and thinned forest stands have lower beetle abundance than unmanaged stands.

Sverdrup-Thygeson and Ims (2002) suggested that one explanation for higher-than-expected species richness in harvested sites is that there is a possible bias towards collecting higher numbers of individuals in cleared, sun-exposed sites. Beetles tend to be more active and evident in warmer temperatures. There is also the probable preference of saproxylic beetles for sun-exposed CWD, in that both visual cues and wind dispersal favour more open areas for searching out CWD (Jonsell et al. 1998; Kouki et al. 2001; Martikainen 2001). Another possible explanation is that there appears to be a peak in abundance and richness of some families of beetles approximately five years after a disturbance to the forest ecosystem (Wermelinger et al. 2002). In one study, bird species richness also showed a sharp increase 2-6 years after clearcut harvest (Keller et al. 2002). Conversely, it may be that conventional wisdom of equating higher species diversity with older-aged stands requires some refinement, particularly in northern-temperate and boreal forests with extensive disturbance histories.

In the present study, beetle species composition was significantly different between harvested and unharvested sites. There were variations in tree species as well as general stand characteristics between different sites. For example, site 5 had a considerably larger quantity of red maple CWD and much thinner overstory than any other site. The results show that site 5 is responsible for much of the variation among the harvested sites. It is also possible that the differences in species assemblages were related to the proportions of decay classes or sizes of CWD present in harvested versus unharvested sites.

Although freshly killed wood has a lower diversity of habitats for saproxylic beetles than old dead wood, there is a specific trophic group (phloeophagous species) of beetles that feed on the former (Hammond et al. 2004). Kruys and Jonsson (1999) found that fine woody debris was important for species richness of particular taxa of cryptogams in managed boreal spruce forests in northern Sweden. These two aspects could account for the significant difference in species composition between harvested and unharvested sites. They may also be related to differences (although in the present study this measure is not statistically significant) in trophic categories present in harvested and unharvested sites.

Despite a higher number of beetle species in the harvested sites of the present study, both studies showed statistically significant differences in species composition of harvested versus unharvested sites. Many studies have indicated that invertebrates are often more sensitive to environmental change than vascular plants or vertebrates and will therefore respond more quickly to such changes (Rosenberg et al. 1986; Erhardt and Thomas 1991; Moore 1991; Ehrlich 1992; Kremen et al. 1993). In the case of the two present studies, the response to environmental change was more obvious in the differences in species composition.

Analysis of relationships between CWD and beetle communities

A positive correlation between mean volume of CWD and beetle species richness would not have been new or unexpected (Martikainen et al. 2000; Yee et al. 2001; Grove 2002a). This relationship is often highlighted because forest practices have "resulted in a progressive simplification of stand structure and a loss of mature timber habitat" (Grove 2002b). In this study, however, the relationship was not statistically significant. This may be due to sample size, as both CWD volumes and beetle species richness were significant when measured individually for effects of stand age. However, as noted above these relationships may also require some refinement in the context of northern-temperate and boreal forests with extensive disturbance histories.

Many other studies have shown a positive correlation between dead trees of large diameter and high numbers of beetle species, including many rare species (Vaisanen et al. 1993; Kolstrom and Lumatjarvi 2000; Siitonen 2001). In Great Britain, Alexander (2004) identified 180 saproxylic species (of a total of 694 species in Great Britain) that are indicators of ecological continuity (an inverse of disturbance) and hence are characteristic of undisturbed forests. One hundred and sixty-one of these are variously listed as endangered, vulnerable, rare, or scarce in Great Britain. Indeed, of the full 694 species, 354 species (51%) are in some measure endangered, vulnerable, rare, or scarce (Alexander 2004).

In Canada comparatively less attention has been paid to saproxylic fauna and so it is often difficult to distinguish between genuinely rare species, and those that have simply been rarely collected. Majka (2007b) compiled a list of 59 "apparently rare" species of saproxylic beetles (defined as those species constituting ≤ 0.005% of specimens examined from the region) in the Maritime Provinces of Canada from 14 families, subfamilies and tribes of Coleoptera. These 59 represented 33% of the 178 species found in the region within these groups. Majka (2006a, 2006b, 2007) and Majka and Pollock (2006) have all proposed that this apparent scarcity may be due to the history of forest management practices in the region that have greatly diminished old-growth habitat – practices which have dramatically decreased the amount of large diameter CWD.

In the present study a sizeable number of species were restricted to specific stand ages: 47 species were exclusively found in young stands, 52 species were only found in middle-aged stands and 69 species were exclusively found in old stands. In the latter category, 23 of these 69 species are rarely collected and locally distributed species in Nova Scotia (Table 2). These are candidates for species associated with old-growth forest conditions. Nineteen of them are saproxylic species. In relation to species such as *Stenichus badipes* (Casey), *Bibloporus bicanalis* (Casey), *Batrisodes lineaticollis* (Aubé), *Quedius densiventris* (Casey), *Ampedus protervus* (LeConte), *Dorcatoma falli* White, *Rhizophagus remotus* LeConte, *Silvanus bidentatus* (Fabricius), *Mycetophagus serrulatus* Casey, and Mordellistena *fuscipennis* (Melsheimer), it is noteworthy that Alexander (2004) identifies closely related congeners (or in the case of *S. bidentatus*, the same species) in Great Britain as indicator species of ecological continuity, in other words species of beetles associated with old-growth forest conditions.

In several previous studies, it could not be discerned whether stand age or large-diameter CWD was the explanation for higher diversity in older forest stands (Økland et al. 1996; Hammond et al. 2004). Simila et al. (2003) emphasized the importance of considering the effects of diversity and volume of dead wood on survival and richness of saproxylic species.

In the present study, based on mean volumes of CWD for each stand, there appeared to be no significant differences in beetle species composition. It is possible, however, that an examination of decay classes and diameter sizes of CWD would have a different effect. As CWD passes through different stages of decay, it is colonized by a succession of different beetle assemblages (Speight 1989; Grove 2002a). Beetle communities depend on an array of factors including stage of decomposition, tree species, and type of rot (Grove 2002a).

Management implications

In Canada and the United States, intensive silvicultural treatment has not been as complete as in most parts of Europe (Kimmins 1997). The North American forest industry may not have affected the diversity of saproxylic beetles within their forests to the same extent as has occurred in many European countries, nevertheless, ongoing anthropogenic disturbances to Nova Scotian forest ecosystems have the potential for significant impact on saproxylic insect communities. Commercial thinnings in softwood stands in south western Nova Scotia appear, however, not to have the pronounced negative effects that have been demonstrated in clearcuts elsewhere.

Particularly careful attention was paid in this study to species determinations. Informed conservation and management strategies must be based in accurate species- and population-based data. Goldstein (1999) argued forcefully that any ecosystem approach that decouples species- and population-specific requirements from management strategies, risks compromising fundamental conservation objectives. Furthermore, as Wheeler (1995) pointed out, accurate taxonomic work is indispensable to conservation decisions. "'Fast and dirty' taxonomy will not remove the taxonomic roadblock; it will simply add to it" (Wheeler 1995).

In terms of the conservation of beetle species diversity, the results of this study agree with those of Kaila et al. (1997). To conserve the highest proportion of the saproxylic beetle fauna, we should maintain a variety of habitats including both young and old forest stands. For example, in this study, 15 species (4%) were common to all young stands, 25 species (7%) were common to all medium-aged stands, and 16 species (5%) were common to all old stands.

The 23 rarely collected and locally distributed species found in old-growth forests in the present study may be representative of a suite of beetles whose success and survival may depend on the presence of old-growth forests. Some of the 59 species of saproxylic beetles identified by Majka (2007b) may represent species already reduced to "relict" populations in the region by the long history of forest management practices.

Management programs that ignore old-growth forests and the suite of insects dependant on them may impoverish the species diversity of Nova Scotia's forest ecosystems. Considering that saproxylic beetles, as important mechanical wood decomposers, are responsible for substantial amount nutrient cycling and decomposition in forest ecosystems, loss of this diversity may have adverse consequences. For instance, when both saproxylic invertebrates and fungi are present, in northern climates the decomposition phase of wood is in excess of 25 years (Ehnström 1979). An absence of saproxylic invertebrates causes the decomposition phase of wood (mediated solely by fungi) to be doubled in length (Dajoz 1980; Speight 1989). As a result, general forest health and sustainability of forest use, including product extraction, may be at risk.

Further research

Globally, patterns of biodiversity remain poorly documented (Mittermeier et al. 1999). Many studies have used taxonomic groups with large-bodied species, such as birds, mammals, and vascular plants, to infer general patterns (Myers 1988, 1990; Myers et al. 2000). However, these groups make up only a tiny fraction of the world's species richness and although the estimates obtained are useful, it is doubtful that these groups truly reflect the species richness of other groups, which are less well-studied but far more species-rich (May 1988; Heywood 1995; Lawton et al. 1998).

There is an unquestionable need for lists of indicator species of forest health, especially as the demand for forest products increases and silviculture becomes more intense. Nilsson et al. (1995) suggested that forest continuity has important implications for forest condition. Forest continuity, however, is a property that may be difficult to construe from present forest structure (Nilsson et al. 1995).

The role of saproxylic beetles in forest ecosystems, the need for their conservation, and their possible use as indicators, are well documented in Europe (Speight 1989, Wermelinger et al. 2002 Simila et al. 2003; Alexander 2004). However, studies of saproxylic beetles in the Acadian forests (Kehler et al. 2004; Bishop 1998) are still very few in number.

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Appendix 1. Species, trophic categories, and numbers of Coleoptera collected

Family	Subfamily	Species	Trophic Category	SX	#
Carabidae	Nebrinae	*Notiophilus aeneus* (Herbst)	Predaceous	1	1
	Carabinae	*Sphaeroderus canadensis* Chaudoir	Predaceous		8
	Trechinae	*Tachyta angulata* Casey	Predaceous	1	13
	Harpalinae	*Gastrellarius honestus* (Say)	Predaceous	1	1
		Pterostichus adstrictus Eschscholtz*	Predaceous	1	12
		Pterostichus coracinus (Newman)	Predaceous	1	54
		Pterostichus pensylvanicus LeConte	Predaceous	1	96
		Pterostichus tristis (Dejean)	Predaceous	1	143
		Anisodactylus nigerrimus (Dejean)	Predaceous		1
		Harpalus affinis Schrank†	Predaceous		1
		Calathus ingratus Dejean	Predaceous	1	25
		Synuchus impunctatus (Say)	Phytophagous		132
		Agonum fidele Casey	Predaceous		1
		Platynus decentis (Say)	Predaceous	1	1
		Cymindis cribricollis Dejean	Predaceous	1	8
		Cymindis limbatus Dejean	Predaceous	1	17
		Syntomus americanus (Dejean)	Predaceous	1	2
Hydrophilidae	Sphaeridiinae	*Cercyon haemorrhoidalis* (Fabricius)†	Saprophagous		1
		Cercyon minusculus Melsheimer	Saprophagous		2
Histeridae	Abraeinae	*Plegaderus sayi* Marseul	Predaceous	1	6
	Saprininae	*Gnathoncus barbatus* Bousquet & Laplante	Saprophagous		1
	Dendrophilinae	*Paromalus teres* LeConte	Predaceous	1	9
	Histerinae	*Platysoma coarctatum* LeConte	Predaceous	1	1
		Margarinotus cognatus (LeConte)	Saprophagous		1
		Margarinotus lecontei Wenzel	Saprophagous		3
		Hister furtivus LeConte	Saprophagous		1

Family	Subfamily	Species	Trophic Category	SX	#
Ptiliidae	Ptiliinae	*Cylindroselloides dybasi* Hall	Bolitophagous	1	16
Leiodidae	Leiodinae	*Agathidium fawcettae* Miller & Wheeler	Myxomycophagous	1	13
		Agathidium oniscoides Beauvois	Myxomycophagous	1	1
		Anisotoma discolor (Melsheimer)	Myxomycophagous	1	9
		Anisotoma inops Brown	Bolitophagous	1	18
	Cholevinae	*Catops basilaris* Say	Saprophagous		14
		Catops paramericanus Peck & Cook	Saprophagous		10
		Sciodrepoides terminans (LeConte)	Saprophagous		1
Scydmaenidae		*Brachycepsis subpunctatus* (LeConte)	Predaceous	1	2
		Stenichus badius (Casey)	Predaceous	1	1
		Stenichus turbatus (Casey)	Predaceous	1	5
Silphidae	Silphinae	*Necrophila americana* (Linnaeus)	Saprophagous		1
Staphylinidae	Omaliinae	*Phloeonomus laesicollis* (Mäklin)*	Predaceous	1	1
		Phloeostiba lapponicus (Zetterstedt)	Sap Feeder		1
		Pycnoglypta aptera Campbell†	Predaceous	1	1
		Eusphalerum convexum (Fauvel)	Pollen Feeder	1	3
		Eusphalerum pothos (Mannerheim)	Pollen Feeder	1	4
	Proteininae	*Megarthrus americanus* Sachse	Mycetophagous	1	1
	Pselaphinae	*Biblioporus bicanalis* (Casey)	Predaceous	1	1
		Euplectus elongatis Brendel	Predaceous	1	1
		Pycnoplectus linearis (LeConte)	Predaceous	1	1
		Biblioplectus integer (LeConte)	Predaceous	1	1
		Batrisodes lineaticollis (Aubé)	Predaceous	1	6
		Rybaxis conjuncta (LeConte)	Predaceous	1	4
	Phloeocharinae	*Charhyphus picipennis* (LeConte)	Predaceous	1	3
	Tachyporinae	*Sepedophilus crassus* (Gravenhorst)	Mycetophagous	1	8
		Sepedophilus littoreus (Linnaeus)	Mycetophagous	1	2

Family	Subfamily	Species	Trophic Category	SX	#
		Tachinus basalis Erichson*	Predaceous	1	1
		Tachinus fimbriatus Gravenhorst†	Predaceous	1	14
		Tachinus luridus Erichson	Predaceous	1	1
		Tachinus picipes Erichson	Predaceous	1	12
		Tachyporus nitidulus (Fabricius)	Predaceous	1	2
		Lordithon bimaculatus (Couper)	Predaceous	1	1
		Lordithon facilis (Casey)*	Predaceous	1	6
		Lordithon fungicola Campbell†	Predaceous	1	3
		Lordithon t. thoracicus (Fabricius)	Predaceous	1	1
		Mycetoporus consors LeConte	Predaceous	1	1
	Aleocharinae	*Aleochara castaneipennis* Mannerheim	Predaceous	1	3
		Oxypoda amica Casey	Mycetophagous	1	1
		Amarochara species	Mycetophagous	1	3
		Silusida marginella Casey	Mycetophagous	1	9
		Eumicrota socia (Erichson)	Mycetophagous	1	10
		Gyrophaena affinis Sahlberg†	Bolitophagous	1	6
		Gyrophaena flavicornis Melsheimer	Bolitophagous	1	5
		Gyrophaena sculptipennis Casey	Bolitophagous	1	2
		Leptusa brevicollis Casey	Mycetophagous	1	21
		Leptusa canonica Casey	Mycetophagous	1	5
		Leptusa opaca Casey	Mycetophagous	1	1
		Leptusa pseudopaca Klimaszewski & Majka	Mycetophagous	1	2
		Leptusa species	Mycetophagous	1	3
		Placusa tacomae Casey	Mycetophagous	1	1
		Atheta klagesi Bernhauer	Mycetophagous	1	7
		Atheta remulsa Casey	Mycetophagous	1	1
		Atheta (Microdota) pennsylvanica Bernhauer	Mycetophagous	1	8

Family	Subfamily	Species	Trophic Category	SX	#
		Atheta (Datomicra) dadopora Thomson†	Mycetophagous	1	1
		Atheta (Datomicra) hampshirensis (Bernhauer)	Mycetophagous	1	2
		Atheta (Datomicra) inopia Casey	Mycetophagous	1	2
		Atheta (Datomicra) modesta (Melsheimer)	Mycetophagous	1	19
		Aleocharine species 2	Mycetophagous		2
		Aleocharine species 3	Mycetophagous		1
		Aleocharine species 4	Mycetophagous		1
	Scaphidinae	*Baeocera youngi* (Cornell)	Mycetophagous	1	2
		Scaphisoma rubens Casey	Mycetophagous	1	1
	Piestinae	*Siagonium punctatum* LeConte	Mycetophagous	1	3
	Paederinae	*Medon nr. rufipenne* (Casey)	Predaceous	1	1
		Sunius confluentus (Say)	Predaceous	1	6
		Palaminus hudsonicus Casey	Predaceous	1	2
	Staphylininae	*Atrecus americanus* (Casey)	Predaceous	1	28
		Neohypnus obscurus (Erichson)	Predaceous	1	2
		Nudobius cephalus (Say)	Predaceous	1	7
		Anaquedius vernix (LeConte)	Predaceous	1	1
		Quedius canadensis (Casey)	Predaceous	1	4
		Quedius densiventris (Casey)	Predaceous	1	1
		Quedius plagiatus Mannerheim	Predaceous	1	6
		Platydracus viridanus (Horn)	Predaceous	1	74
		Gabrius microphthalmus (Horn)	Predaceous	1	1
		Gabrius picipennis (Mäklin)	Predaceous	1	2
		Philonthus caeruleipennis Mannerheim	Predaceous	1	4
Lucanidae	Syndescinae	*Ceruchus piceus* (Weber)	Xylophagous	1	5
Trogidae		*Trox variolatus* Melsheimer	Saprophagous		6
Geotrupidae	Geotrupinae	*Geotrupes horni* Blanchard	Saprophagous		33

Family	Subfamily	Species	Trophic Category	SX	#
Scarabaeidae	Aphodinae	*Dialytes striatulus* (Say)	Saprophagous		1
	Scarabaeinae	*Onthophagus hecate* (Panzer)	Saprophagous		2
	Melonthinae	*Serica atracapilla* Kirby	Phytophagous		2
		Dichelonyx albicollis (Burmeister)	Phytophagous		3
		Dichelonyx subvittata (LeConte)	Phytophagous		4
	Cetoniinae	*Osmoderma scabra* Beauvois	Xylophagous	1	1
Clambidae		*Clambus pubescens* Redtenbacher*	Mycetophagous	1	2
Scirtidae		*Cyphon collaris* (Guérin-Méneville)	Saprophytic	1	3
		Cyphon confusus Brown[1]	Saprophytic	1	15
		Cyphon obscurus (Guérin-Méneville)[1]	Saprophytic	1	5
		Cyphon ruficollis (Say)	Saprophytic	1	1
		Cyphon variabilis (Thunberg)[1]	Saprophytic	1	9
Buprestidae	Buprestinae	*Dicerca punctulata* (Schönherr)	Phloeophagous	1	2
		Melanophila fulvoguttata (Harris)	Phloeophagous	1	3
Eucnemidae	Melasinae	*Epiphanis cornutus* (Eschscholtz)	Mycetophagous	1	3
	Macraulacinae	*Onichodon canadensis* (Brown)	Mycetophagous	1	2
Throscidae	Throscinae	*Aulonothroscus constrictor* (Say)	Mycetophagous	1	6
		Trixagus carinicollis (Schaeffer)	Mycetophagous	1	1
Elateridae	Elaterinae	*Sericus incongruus* (LeConte)	Rhizophagous		3
		Sericus viridanus (Say)	Rhizophagous		1
		Agriotella debilis (LeConte)	Rhizophagous		1
		Agriotes collaris (LeConte)	Rhizophagous		10
		Agriotes sputator (Linnaeus)†	Rhizophagous		1
		Agriotes stabilis (LeConte)	Rhizophagous		2
		Dalopius fuscipes Brown	Mycetophagous	1	1
		Dalopius gentilis Brown	Mycetophagous	1	10
		Dalopius vagus Brown	Mycetophagous	1	19

Family	Subfamily	Species	Trophic Category	SX	#
		Ampedus deletus (LeConte)	Xylophagous	1	1
		Ampedus mixtus (Herbst)	Xylophagous	1	3
		Ampedus protervus (LeConte)	Xylophagous	1	1
		Ampedus semicinctus (Randall)	Xylophagous	1	6
		Ampedus subtilis (LeConte)	Xylophagous	1	4
		Melanotus castanipes (Paykull)†	Rhizophagous		8
		Melanotus similis (Kirby)	Rhizophagous		1
	Prosterninae	*Athous acanthus* (Say)	Predaceous	1	1
		Athous brightwelli (Kirby)	Predaceous	1	4
		Athous orvus Becker	Predaceous	1	2
		Limonius aeger LeConte	Rhizophagous		20
		Limonius confusus LeConte	Rhizophagous		13
		Hypoganus sulcicollis (Say)	Predaceous	1	1
		Liotrichus falsificus (LeConte)	Predaceous	1	11
		Liotrichus spinosus (LeConte)	Predaceous	1	31
		Liotrichus vulneratus (LeConte)	Predaceous	1	1
		Pseudanostirus hamatus (Say)	Predaceous	1	3
		Pseudanostirus hieroglyphicus (Say)	Predaceous	1	1
		Pseudanostirus triundulatus (Randall)	Predaceous	1	21
		Setasomus rufopleuralis (Fall)	Predaceous	1	1
		Hypnoidius bicolor (Eschscholtz)*	Rhizophagous		1
	Negastriinae	*Neohypdonus tumescens* (LeConte)	Predaceous		1
Lycidae	Erotinae	*Dictyopterus aurora* (Herbst)	Mycetophagous	1	6
		Eros humeralis (Fabricius)	Mycetophagous	1	6
		Lopheros fraternus (Randall)	Mycetophagous	1	2
	Platoderinae	*Plateros bispiculatus* Green	Mycetophagous	1	1
		Plateros flavoscutellatus Blatchley	Mycetophagous	1	2

Family	Subfamily	Species	Trophic Category	SX	#
		Plateros lictor (Newman)	Mycetophagous	1	3
Lampyridae	Lampyrinae	*Ellychnia corrusca* (Linnaeus)	Predaceous	1	16
		Photinus obscurellus LeConte	Predaceous	1	1
Cantharidae	Cantharinae	*Cantharis rotundicollis* Say	Pred./Nectarivorous		5
		Rhagonycha fraxini (Say)	Pred./Nectarivorous		1
		Rhagonycha mandibularis (Kirby)	Pred./Nectarivorous		25
		Rhagonycha scitula (Say)	Pred./Nectarivorous		18
		Atlantycha bilineata (Say)	Pred./Nectarivorous		1
		Podabrus diadema (Fabricius)	Predaceous		9
		Podabrus modestus (Say)	Predaceous		2
		Podabrus pattoni LeConte	Predaceous		7
		Podabrus puberulus LeConte	Predaceous		12
		Malthodes similis Fender	Predaceous		2
Derodontidae	Laricobiinae	*Laricobius rubidus* LeConte	Predaceous	1	1
Anobiidae	Anobiinae	*Hemicoelus carinatus* (Say)	Xylophagous	1	1
		Microbregma e. emarginatum (Duftschmid)†	Xylophagous	1	1
		Hadrobregmus notatus (Say)	Xylophagous	1	1
	Dorcatominae	*Caenocara oculata* (Say)	Xylophagous	1	2
		Dorcatoma falli White	Xylophagous	1	1
		Dorcatoma pallicornis LeConte	Xylophagous	1	3
Trogossitidae	Trogossitinae	*Airora cylindrica* (Audinet-Serville)	Mycetophagous	1	1
Cleridae	Thaneroclerinae	*Zenodosus sanguineus* (Say)	Predaceous	1	16
	Hydnocerinae	*Phyllobaenus humeralis* (Say)	Predaceous	1	1
	Clerinae	*Thanasimus dubius* (Fabricius)	Predaceous	1	3
		Thanasimus undatulus (Say)	Predaceous	1	23
Sphindidae	Odontosphindinae	*Odontosphindus denticollis* LeConte	Myxomycophagous	1	1
	Sphindinae	*Sphindus americanus* LeConte	Myxomycophagous	1	5

Family	Subfamily	Species	Trophic Category	SX	#
Nitidulidae	Cillaeinae	*Colopterus truncatus* (Randall)	Sap Feeder	1	1
	Epuraeinae	*Epuraea aestiva* (Linnaeus)	Sap Feeder	1	1
		Epuraea planulata Erichson	Sap Feeder	1	2
		Epuraea rufida (Melsheimer)	Sap Feeder	1	1
	Nitidulinae	*Phenolia grossa* (Fabricius)	Bolitophagous	1	4
	Cryptarchinae	*Glischrochilus fasciatus* (Olivier)	Sap Feeder	1	1
		Glischrochilus sanguinolentus (Olivier)	Sap Feeder	1	4
		Glischrochilus siepmanni Brown	Sap Feeder	1	4
Monotomidae	Rhizophaginae	*Rhizophagus remotus* LeConte	Predaceous	1	1
Silvanidae	Brontinae	*Dendrophagus cygnaei* Mannerheim	Mycetophagous	1	2
	Silvaninae	*Silvanus bidentatus* (Fabricius)†	Mycetophagous	1	2
Cucujidae		*Cucujus c. clavipes* Fabricius	Predaceous	1	1
Laemophloeidae	Laemophloeinae	*Laemophloeus biguttatus* (Say)	Mycetophagous	1	2
Cryptophagidae	Cryptophaginae	*Henotiderus obesulus* (Casey)	Mycetophagous	1	1
		Pteryngium crenatum (Gyllenhal)†	Mycetophagous	1	10
	Atomariinae	*Atomaria ephippiata* Zimmerman	Mycetophagous	1	1
		Atomaria ochracea Zimmerman[2]	Mycetophagous	1	5
Erotylidae	Tritominae	*Tritoma pulchra* Say	Bolitophagous	1	1
Cerylonidae	Ceryloninae	*Cerylon castaneum* Say	Mycetophagous	1	8
		Cerylon unicolor (Ziegler)	Mycetophagous	1	12
Endomychidae	Leiestinae	*Phymaphora pulchella* Newman	Mycetophagous	1	3
Coccinellidae	Scymninae	*Stethorus p. punctum* (LeConte)	Predaceous		1
		Scymnus brullei Mulsant	Predaceous		1
		Scymnus lacustris LeConte	Predaceous		4
Corylophidae	Orthoperinae	*Orthoperus suturalis* LeConte	Mycetophagous	1	1
Latridiidae	Latridiinae	*Cartodere constricta* (Gyllenhal)†	Mycetophagous	1	3
		Enicmus tenuicornis LeConte	Mycetophagous	1	1

Family	Subfamily	Species	Trophic Category	SX	#
	Corticariinae	*Corticaria impressa* (Olivier)†	Mycetophagous	1	1
		Corticaria serrata (Paykull)†	Mycetophagous	1	1
		Corticarina cavicollis (Mannerheim)	Mycetophagous	1	1
		Cortinicara gibbosa (Herbst)†	Mycetophagous	1	1
		Melanophthalma americana (Mannerheim)	Mycetophagous	1	4
		Melanophthalma pumila (LeConte)	Mycetophagous	1	11
Mycetophagidae		*Mycetophagus serrulatus* Casey	Bolitophagous	1	1
		Litargus tetraspilotus LeConte	Mycetophagous	1	2
Ciidae	Ciinae	*Ceracis sallei* Mellié	Bolitophagous	1	1
		Cis horridulus Casey	Bolitophagous	1	3
		Cis levettei (Casey)	Bolitophagous	1	26
		Cis pistoria Casey	Bolitophagous	1	8
		Malacocis brevicollis (Casey)	Bolitophagous	1	12
		Orthocis punctatus (Mellié)	Bolitophagous	1	6
Tetratomidae	Penthinae	*Penthe obliquata* (Fabricius)	Bolitophagous	1	8
		Penthe pimelia (Fabricius)	Bolitophagous	1	1
	Eustrophinae	*Eustrophus tomentosus* Say	Bolitophagous	1	2
Melandryidae	Melandryinae	*Orchesia castanea* (Melsheimer)	Xylophagous	1	1
		Xylita laevigata (Hellenius)*	Xylophagous	1	1
		Scotochroa atra LeConte	Xylophagous	1	1
		Scotochroides antennatus Mank	Xylophagous	1	4
		Serropalpus coxalis Mank	Xylophagous	1	1
		Serropalpus substriatus Haldeman	Xylophagous	1	1
		Dircaea liturata (LeConte)	Xylophagous	1	1
		Phloiotrya fusca (LeConte)	Xylophagous	1	1
		Hypulus simulator Newman	Xylophagous	1	1
		Microtonus sericans LeConte	Xylophagous	1	11

Family	Subfamily	Species	Trophic Category	SX	#
		Symphora flavicollis (Haldeman)	Xylophagous	1	3
		Symphora rugosa (Haldeman)	Xylophagous	1	2
Mordellidae		*Mordellistena fuscipennis* (Melsheimer)	Phytophagous		2
		Mordellistena trifasciata (Say)	Phytophagous		1
Colydiidae		*Lasconotus borealis* Horn	Predaceous	1	1
Zopheridae		*Phellopsis obcordata* (Kirby)	Bolitophagous	1	13
Tenebrionidae	Lagriinae	*Arthromacra aenea* (Say)	Mycetophagous	1	2
		Paratenetus undescribed species[3]	Saprophagous	1	4
	Bolitophaginae	*Bolitophagus corticola* Say	Bolitophagous	1	9
		Bolitotherus cornutus (Panzer)	Bolitophagous	1	14
	Diaperinae	*Diaperis maculata* Olivier	Bolitophagous	1	3
		Neomida bicornis (Fabricius)	Bolitophagous	1	1
		Scaphidema aeneolum (LeConte)	Saprophagous	1	3
	Hypophloeinae	*Corticeus praetermissus* (Fall)	Predaceous	1	1
	Tenebrioninae	*Centronopus calcaratus* (Fabricius)	Xylophagous	1	1
	Alleculinae	*Hymenorus niger* (Melsheimer)	Mycetophagous	1	2
		Capnochroa fuliginosa (Melsheimer)	Mycetophagous	1	3
		Isomira quadristriata (Couper)	Mycetophagous	1	52
	Coleometopinae	*Iphthiminus opacus* (LeConte)	Saprophagous	1	1
		Upis ceramboides (Linnaeus)*	Saprophagous	1	5
Stenotrachelidae	Cephaloinae	*Cephaloon lepturides* Newman	Mycetophagous	1	1
Pythidae		*Pytho niger* Kirby	Xylophagous	1	1
		Pytho americanus Kirby	Xylophagous	1	4
		Prionathus monilicornis (Randall)	Xylophagous	1	5
Pyrochroidae	Pyrochroinae	*Dendroides canadensis* Latreille	Mycetophagous	1	1
Aderidae	Aderinae	*Vanonus wickhami* Casey	Xylophagous	1	20
Scraptiidae	Scraptiinae	*Canifa pallipes* (Melsheimer)	Mycetophagous	1	4

Family	Subfamily	Species	Trophic Category	SX	#
		Canifa pusilla (Haldeman)	Mycetophagous	1	9
	Anaspidinae	*Anaspis flavipennis* Haldeman	Mycetophagous	1	11
		Anaspis nigrina Csiki	Mycetophagous	1	1
		Anaspis rufa Say	Mycetophagous	1	27
Cerambycidae	Aseminae	*Asemum striatum* (Linnaeus)	Phloeophagous	1	3
		Tetropium cinnamopterum Kirby	Phloeophagous	1	2
	Lepturinae	*Anthophylax attenuatus* (Haldeman)	Phloeophagous	1	10
		Anthophylax cyaneus (Haldeman)	Phloeophagous	1	3
		Evodinus m. monticola (Randall)	Phloeophagous	1	4
		Idiopidonia pedalis (LeConte)	Phloeophagous	1	2
		Judolia m. montivagans (Couper)	Phloeophagous	1	1
		Lepturopsis biforis (Newman)	Phloeophagous	1	1
		Pidonia ruficollis (Say)	Phloeophagous	1	1
		Pygoleptura n. nigrella (Say)	Phloeophagous	1	1
		Rhagium inquisitor (Linnaeus)	Phloeophagous	1	3
		Sachalinobia r. rugipennis (Newman)	Phloeophagous	1	1
		Stictoleptura c. canadensis (Olivier)	Phloeophagous	1	1
		Strangalepta abbreviata (Germar)	Phloeophagous	1	11
		Trachysida aspera brevifrons (Howden)	Phloeophagous	1	1
	Cerambycinae	*Clytus marginicollis* Castelnau & Gory	Phloeophagous	1	1
		Xylotrechus undulatus (Say)	Phloeophagous	1	3
	Lamiinae	*Microgoes oculatus* (LeConte)	Phloeophagous	1	1
		Monochamus s. scutellatus (Say)	Phloeophagous	1	6
		Pogonocherus penicillatus LeConte	Phloeophagous	1	2
		Psenocerus supernotatus (Say)	Phloeophagous	1	1
		Sternidius variegatus (Haldeman)	Phloeophagous	1	1
Chrysomelidae	Chrysomelinae	*Phratora americana canadensis* Brown	Phytophagous		1

Family	Subfamily	Species	Trophic Category	SX	#
		Phratora p. purpurea Brown	Phytophagous		9
		Chrysomela m. mainensis Bechyné	Phytophagous		1
	Galerucinae	*Scelolyperus cyanellus* (LeConte)	Phytophagous		4
		Altica ambiens LeConte	Phytophagous		4
		Altica kalmiae Melsheimer	Phytophagous		1
	Eumolpinae	*Syneta extorris borealis* Brown	Phytophagous		7
		Syneta ferruginea (Germar)	Phytophagous		13
		Syneta pilosa Brown	Phytophagous		1
		Paria fragariae kirki Balsbaugh	Phytophagous		1
		Xanthonia decemnotata (Say)	Phytophagous		4
	Cryptocephalinae	*Neochlamisus bebbianae* (Brown)	Phytophagous		1
Nemonychidae	Cimberidinae	*Cimberis elongata* (LeConte)	Phytophagous		6
		Cimberis pallipennis (Blatchley)	Phytophagous		1
Curculionidae	Dryophthorinae	*Dryophthorus americanus* Bedel	Xylophagous	1	1
	Curculioninae	*Anthonomus signatus* Say	Phytophagous		1
	Conoderinae	*Lechriops oculata* (Say)	Phytophagous		2
	Cossoninae	*Carphonotus testaceus* Casey	Xylophagous	1	10
		Himatium errans LeConte	Xylophagous	1	12
		Rhyncolus brunneus Mannerheim	Xylophagous	1	18
	Entiminae	*Otiorhynchus singularis* (Linnaeus)†	Rhizophagous		8
		Otiorhynchus sulcatus (Fabricius)†	Rhizophagous		1
		Nemocestes horni Van Dyke	Phytophagous		1
		Polydrusus impressifrons (Gyllenhal)†	Phytophagous		1
		Polydrusus sericeus (Schaller)†	Phytophagous		3
		Sciaphilus asperatus (Bonsdorff)†	Phytophagous		5
	Molytinae	*Conotrachelus posticatus* Boheman	Phytophagous		2
		Hylobius congener Dalla Torre et al.	Rhizophagous		11

Family	Subfamily	Species	Trophic Category	SX	#
		Hylobius pales (Herbst)	Rhizophagous		2
		Pissodes affinis Randall	Phytophagous		3
		Pissodes fiskei Hopkins	Phytophagous		70
		Pissodes striatulus (Fabricius)	Phytophagous		1
		Pissodes strobi (Peck)	Phytophagous		4
	Scolytinae	*Hylurgops rugipennis pinifex* (Fitch)	Phloeophagous	1	4
		Dendroctonus simplex LeConte	Phloeophagous	1	1
		Dendroctonus valens LeConte	Phloeophagous	1	1
		Polygraphus rufipennis (Kirby)	Phloeophagous	1	58
		Pityogenes hopkinsi Swaine	Phloeophagous	1	3
		Pityokteines sparsus (LeConte)	Phloeophagous	1	3
		Orthotomicus caelatus (Eichhoff)	Phloeophagous	1	2
		Ips pini (Say)	Phloeophagous	1	2
		Dryocoetes affaber (Mannerheim)	Phloeophagous	1	18
		Dryocoetes autographus (Ratzeburg)	Phloeophagous	1	19
		Crypturgus borealis Swaine	Phloeophagous	1	37
		Crypturgus pusillus (Gyllenhal)†	Phloeophagous	1	22
		Trypodendron lineatum (Olivier)*	Mycetophagous	1	12
		Xyloterinus politus (Say)	Mycetophagous	1	4
		Conophthorus coniperda (Schwartz)	Phloeophagous	1	2
		Pityophthorus cariniceps LeConte	Phloeophagous	1	1
		Gnathotrichus materarius (Fitch)	Phloeophagous	1	1
		Monarthrum mali (Fitch)	Phloeophagous	1	1
Totals				264	2303

Notes: Families, subfamilies, and species are listed in taxonomic order.†, adventive Palaearctic species; * Holarctic species; no symbol, Nearctic species. Saproxylic (SX column): 1, included as a saproxylic species; no entry, not included. #, number of specimens collected.

[1] The species of *Cyphon* in the Maritime Provinces of Canada are currently being revised by C.G. Majka and B. Klausnitzer (in preparation). The designation and nomenclature of these species may change in that forthcoming revision.

[2] The species of the genus *Atomaria* in the Maritime Provinces of Canada are currently being revised by C.G. Majka and C. Johnson (in preparation). The nomenclature of this species will change in this forthcoming revision.

[3] This undescribed species of *Paratenetus* (previously included within *Paratenetus fuscus* LeConte) will be described in a forthcoming publication by P. Bouchard and Y. Bousquet (in preparation).